FINAL REPORT

Predicting, Measuring, and Monitoring Aquatic Invertebrate Biodiversity on Dryland Military Bases

SERDP Project RC-2203

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14. ABSTRACT
Aquatic habitats are among the most imperiled habitats on dryland military installations, yet they harbor a disproportionately high amount of biodiversity given the small land area they cover. Aquatic invertebrates (insects and allied taxa) constitute a major part of this biodiversity and form a critical part of the food web that sustains aquatic, riparian, and terrestrial organisms, including Federally Threatened or Endangered species. Biodiversity in dryland aquatic habitats is strongly influenced by spatial and temporal variability, which presents challenges for predicting how management decisions on military lands could affect landscape-scale patterns of aquatic invertebrate biodiversity. This project integrates mathematical modeling, invertebrate sampling, and statistical estimation to understand and measure biodiversity of aquatic invertebrates on dryland military bases.

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List of Acronyms

BLM: Bureau of Land Management
DDR: Distance-decay relationship
DFC: Desert Fishes Council
DoD: Department of Defense
EPA: Environmental Protection Agency
EPT: Ephemeroptera, Plecoptera, Coleoptera
ER: Electrical Resistance
ESA: Ecological Society of America; also Endangered Species Act
FEve: functional evenness
FTN: functional trait niche
FRic: functional richness
GCM: Global Circulation Model
GIS: Geographic Information System
IPCC: Intergovernmental Panel on Climate Change
MCMC: Markov chain Monte Carlo
MSI: Madrean Sky Island
NAWS: Naval Air Weapons Station
NOAA: National Oceanic and Atmospheric Association
NWR: National Wildlife Refuge
OCH: Odonata, Coleoptera, Hemiptera
SCHC: spatial configuration of habitat capacity
SFS: Society for Freshwater Science
SWAT: Soil Water Assessment Tool
USDA: United States Department of Agriculture
USGS: United States Geological Survey
WSMR: White Sands Missile Range

Keywords

Biodiversity, neutral metacommunity models, niche-based models, aquatic invertebrates, sampling theory, artificial neural networks, Odonata, Hemiptera, Coleoptera.

Acknowledgements

Summary and management recommendations

Objectives. Aquatic habitats are among the most imperiled habitats on dryland military installations, yet they harbor a disproportionately high amount of biodiversity given the small land area they cover. Aquatic invertebrates (insects and allied taxa) constitute a major part of this biodiversity and form a critical part of the food web that sustains aquatic, riparian, and terrestrial organisms, including Federally Threatened or Endangered species. Biodiversity in dryland aquatic habitats is strongly influenced by spatial and temporal variability, which presents challenges for predicting how management decisions on military lands could affect landscape-scale patterns of aquatic invertebrate biodiversity. This project integrates mathematical modeling, invertebrate sampling, and statistical estimation to understand and measure biodiversity of aquatic invertebrates on dryland military bases.

The interplay of niche-based and neutral models is a central theme of this project. Our intent is to use both of these methods to determine optimal management techniques across aridland ecosystems. We describe the development of the core models to be used for this purpose. We also emphasize the importance of using trait analysis to make general inferences that cross taxonomic boundaries.

Technical approach. Our effort assembled an extensive dataset of invertebrate biodiversity patterns through space and time, replicated across three military installations spanning three different physiogeographic provinces: White Sands Missile Range in New Mexico, Fort Huachuca in Arizona, and NAWS China Lake in California. Thus far, we have identified an extraordinary diversity of aquatic invertebrates with our sampling, approaching 400 taxa. This is a high amount of biodiversity for a type of habitat that is relatively rare in the landscape. We have also discovered major range extensions of known taxa and possible new species on these military lands.

Our effort developed both neutral and niche-based models that are useful for understanding how species occurrences and patterns of biodiversity are distributed across variable landscapes, such as the aridland stream networks present on many large military installations in the western US.

Results. From a modeling perspective, our niche-based models show the importance of stream hydrology and other abiotic factors in determining the distribution and detectability of species. A surprising number of taxa appear to be detectable in one season or microhabitat but not in others. This presents substantial challenges to installation resource managers, who need reliable information on species distributions and abundances in order to make informed management decisions. Niche-based methods can also allow us to determine the temporal and environmental conditions under which species are likely to be present and detectable, but given the number of physical variables involved, this is not a simple task to execute.

Conversely, our neutral models revealed some surprising findings about patterns of alpha diversity (within sites) and beta diversity (among sites) across the landscape. First, we have found a strong effect of habitat capacity (the size of a specific site, in terms of the number of individuals it can harbor) on beta diversity. This pattern is important because it means that differences in habitat capacity among sites can distort measured biodiversity patterns. It is especially relevant to aridland aquatic habitats, because these habitats can differ in capacity by several orders of magnitude (from small isolated seeps to large river systems). This finding is of great importance to general biodiversity studies, and we have published it as a stand-alone paper in addition to implementing it into our larger project. Second, our neutral models showed that neutral biodiversity processes are more important under extreme hydrological conditions (high water and drought) versus more mesic conditions. Thus, the interplay between niche processes (which depend on the traits of individual species) and neutral processes (which are driven by stochastic processes of immigration and local extinction) appear to be mediated by hydrology.

Benefits and management recommendations. While our data collection and model development has revealed findings relevent to general ecology, especially in aridland aquatic ecosystems, we can make general recommendations pertinent to the management of aridland aquatic ecosystems, especially as they pertain to the three military installations studied here.

1. The hydroperiod of a particular site strongly determines the species pool of that particular site. In nearly all of our modeling efforts, hydroperiod was a strong explanatory variable. Thus, sites that are perennial have a unique character and species pool that sets them apart from intermittent sites, and vice-versa. Care should be taken to ensure that perennial sites retain this character and do not become intermittent due to groundwater pumping or diversions. Conversely, naturally-intermittent sites can sometimes harbor a unique fauna, and it may not be advisable to change them to a perennial hydroperiod via artificial dams or impoundments. Hydroperiod of sites can be monitored with ER sensors such as those deployed in our study.

2. The dispersal ability of taxa strongly influences their distribution on the landscape. Taxa with little or no mobility contribute to unique community structures, much in the same way that low-dispersal taxa often have unique genetic structures across the landscape (as revealed in SERDP RC-1724). Thus, taxa that are known to be poor dispersers, including some hemipteran bugs such as belostomatids and naucorids, should be managed with particular care. Trait databases such as the one generated by Schriever et al. (2015) are a valuable management tool for determining the dispersal ability of particular species.

3. In aridland and desert ecosystems, much dispersal occurs overland via aerial dispersal, as opposed to within the stream network. For this reason, springs and off-channel habitats that are seemingly disjunct from other habitats may play an important role in maintaining the overall biodiversity of a particular region.

4. The habitat capacity of a site plays an important role in biodiversity. Our neutral modeling revealed that large-sized habitats -- such as larger ponds, or more contiguous reaches of stream -- operate in fundamentally different ways than smaller habitats. In general, larger sites harbor greater biodiversity, but our results caution that smaller sites may be important for maintaining biodiversity at a broader landscape level. Thus, aridland aquatic habitats should be managed as a catchment-level matrix of diverse aquatic habitats, rather than as disjunct points on the landscape.

1 Generation of aquatic invertebrate biodiversity database

1.1 Initial site visits with base managers

Goal: To establish strong working relationships with installation resource managers; to identify viable study sites.

Site visits were completed in March and April 2012 with the assistance of Sheridan Stone (Fort Huachuca), Junior Kerns (White Sands Missile Range), and Tom Campbell (NAWS China Lake) and other base support personnel and biologists. Potential sites were identified using USGS topographic maps, installation documents, and expert knowledge from base managers. At each base, we were escorted for two to three days to all prospective sites where we took pilot samples for processing.

1.2 Field sampling of aquatic insects

Goal: To collect aquatic invertebrate samples and metadata that will form the core data for our neutral and niche-based modeling efforts.

Site selection and study design. We selected two catchments at each installation and identified all potential aquatic habitats within each catchment, including springs, wetlands, and ponds that do not have direct surface hydrological connection to streams. From this comprehensive list of potential sites, we used stratified random sampling by key environmental factors (microhabitat type, flow characteristics, elevation) to sample a subset of sites (approximately 20 per catchment) (Figure 1.1). In some locations, this density of sampling resulted in coverage of every water feature present within the catchment. Study sites have been resampled twice yearly (spring and fall) from 2012 through 2013 as planned in our proposal, and in some cases augmented with further sampling during 2014.

Figure 1.1 Collection and field processing of aquatic invertebrate samples at an intermittent-flow site at Great Falls Basin - China Lake (left to right: PhD students Ohms and Hartfield-Kirk, post-doc Schriever).

Sample collection. We sampled microhabitats (i.e., riffles, pools, springs, pond benthos and pelagic zones) using D-nets fitted with 500 micron mesh netting (Bogan & Lytle 2007). Sampling was conducted in at least two seasons in two years to ensure capture of within and among-year variability, for a total of 691 samples collected across all three bases (

Table 1.1). Where logistics allowed, we collected samples beyond the two-year time frame outlined in the original proposal. Repeat sampling within single microhabitats (without replacement) was used at a subset of sites to estimate species accumulation curves. This rarefaction analysis (Gotelli & Colwell 2001) was used to further guide sampling effort. All aquatic invertebrates that exceed the 500 micron mesh size were collected, which includes most aquatic insects and macroinvertebrates but excludes smaller crustaceans such as copepods, cladocerans, and other zooplankton. We recorded standard point habitat and water quality measurements for each site (flow, substrate, wetted area, habitat dimensions, temperature, pH) as well as reach-scale attributes (vegetation cover, channel morphology).

Table 1.1 Site visits and sample collections at NAWS China Lake, Fort Huachuca, and White Sands Missile Range.

Installation	Sample dates	Number of samples	Processed?	Identified?
NAWS China Lake, CA	Spring 2012	16	Y	Y
	Fall 2012	41	Y	Y
	Spring 2013	45	Y	Y
	Fall 2013	37	Y	Y
	Spring 2014	47	Y	Y
Subtotal:		186		
Fort Huachuca, AZ	Spring 2012	21	Y	Y
	Summer 2012	21	Y	Y
	Fall 2012	52	Y	Y
	Spring 2013	52	Y	Y
	Fall 2013	55	Y	Y
	Spring 2014	48	Y	Y
	Fall 2014	73	Y	Y
Subtotal:		322		
White Sands Missile Range, NM	Spring 2012	14	Y	Y
	Fall 2012	40	Y	Y
	Spring 2013	41	Y	Y
	Fall 2013	44	Y	Y
	Spring 2014	44	Y	Y
Subtotal:		183		
TOTAL:		691		

Quantifying flow intermittence. We used electrical resistance (ER) sensors to quantify network-scale longitudinal connectivity. Temperature loggers are customized to measure relative conductivity (the inverse to resistance) as a proxy for streamflow presence (Jaeger & Olden 2012). Electrical conductivity increases in wet sediments relative to dry sediments, and abrupt increases in relative conductivity values indicate the onset of streamflow. The changes in relative conductivity values are more marked and therefore easier to confidently interpret compared to temperature fluctuations in the thermograph-based approaches with no time delay between the signal of the surface water sensor and the true timing of streamflow.

We installed electrical resistivity sensors on each study drainage at multiple sites (Table 1.2), and also serviced ER sensors that had been deployed on Fort Huachuca as part of RC-1724. The spatial array provides broad representation of perennial, intermittent and ephemeral reaches, which we define following Levick et al. (2008). Perennial reaches are reaches with streamflow during all times of the year. Ephemeral reaches are characterized by short duration streamflow events occurring in direct response to local precipitation. Intermittent reaches flow continuously

for only certain times of the year and are supported by sources such as bedrock springs, melting snow or repeated monsoon events. These water sources locally recharge the water table to produce sustained streamflow with durations that extend beyond the ephemeral runoff response.

Table 1.2 Electrical resistivity detection sensors installed in Huachuca Mountains, AZ, San Andres Mountains, NM, and Argus Range, CA. Flow type is represented by perennial (P), semi-perennial (S-P), intermittent (I), and ephemeral (E) reaches.

Installation	Canyon	Sensor	Drainage	Flow Type	Geology	Nearest landmark
NAWS China Lake, CA	Great Falls Basin	GFB1	Great Falls Basin	S-P	Granite	Upstream of falls
		GFB2	Great Falls Basin	I	Granite	North Fork & Main confluence
		GFB3	Great Falls Basin	I	Granite	Below unnamed USGS spring
		GFB4	Great Falls Basin	P	Granite	Arrastra Spring
	Water	WAT1	Water	P	Volcanic alluvium	
		WAT2	Water	E	Volcanic alluvium	
		WAT3	Water	I		South Fork Water canyon
		WAT4	Water	I	Rock/gravel/limestone	South & Main canyon confluence
Fort Huachuca, AZ	Huachuca	H1A 13	Huachuca	P	Sedimentary/volcanics	Bedrock series of pools
		H1 11	Huachuca	P	Sedimentary/volcanics	
		H2 34	Huachuca	E	Sedimentary/volcanics	
		H3 18	Huachuca	P	Limestone	Across from old landslide site
		H4 28	Huachuca	I	Mixed alluvium	
		H5 30	Huachuca	I	Mixed alluvium	Hynes Park

		H6 64	Huachuca	I	Alluvium	Heritage Park
		H7 63	Huachuca	E	Alluvium	
	McClure	Mc1 39	McClure	E	Limestone	
	Garden	G1 22	Garden	I	Volcanic	Near fault zone
		G2 21	Garden	P	Quartzite	
		G3 14	Garden	P	Limestone	
		G4 15	Garden	P	Limestone	USGS gage
		G5 20	Garden	I	Granite	
		G6 49	Garden	I	Limestone alluvium	
		G7 60	Garden	I	Limestone alluvium	Near fort boundary
White Sands Missile Range, NM	Ash	ASH1	Ash	E	Limestone	
		ASH2	Ash	E	Limestone	
		ASH3	Ash	P	Limestone	Waterfall
		ASH4	Ash	E	Limestone	Upper Ash
	San Andres	SAN1	San Andres	E	Limestone alluvium	Downstream San Andres Spring
		SAN2	San Andres	P	Limestone alluvium	San Andres Spring
	Salt Creek	SC1	Salt creek	S-P	Sand	Bridge crossing on Rd 316

1.3   Sample processing

Goal: To identify aquatic invertebrate samples to the finest taxonomic resolution feasible; to identify management-sensitive and unique taxa; to analyze general biodiversity trends in the data.

Specimen identification. Specimens were identified to the lowest taxonomic unit possible, which was genus or species for most specimens. Although the stated focus of the study was Odonata, Coleoptera, and Hemiptera (the so-called "OCH" fauna), the taxonomic expertise and processing

capacity of our lab group has allowed us to process and identify other parts of most samples with only marginally greater effort, including Ephemeroptera, Plecoptera, and Trichoptera (the "EPT" fauna) and other invertebrate groups. Thus, we have exceeded our original goals in terms of the taxonomic resolution of our dataset. We have identified 339,692 individual specimens across all bases. Total taxonomic diversity (OCH plus any other identified taxa) is 313 at Fort Huachuca, 89 at China Lake, and 131 at White Sands Missile Range.

Discovery of management-sensitive and unusual taxa. During the course of our sample processing we identified potential new species, major range extensions of known taxa, and species that may require specific management practices for persistence. This work is ongoing and is likely to extend beyond the time horizon of the project because it involves the help of taxonomic experts, DNA analysis, and comparison of our sample material with specimens from museums in the USA and abroad. Here, we present two examples of range extensions we have discovered.

The mayfly *Farrodes* (Figure 1.2) is in the order Ephemeroptera and the family Leptophlebiidae and was originally described by Davis (1987). It was previously known in the USA from only one locality in Texas. In our samples we have found over 130+ individuals of *Farrodes* sp. in both Garden Canyon and Huachuca Canyon on Fort Huachuca. The genus identification of *Farrodes* sp. was confirmed by Jeffrey Webb at Rithron Associates, Inc. Dr. Pat Randolph, an Ephemeroptera specialist at University of California – Davis, is examining material to determine if this is a novel species or a range extension. Mayflies are important indicators of water quality and environmental conditions, and may also function as a food sources for terrestrial and aquatic vertebrates.

Figure 1.2 Specimens of a possible new species of *Farrodes* from Fort Huachuca, Arizona, including images of diagnostic morphological features.

The mayfly *Paracloeodes* (Figure 1.3) is in the order Ephemeroptera and the family Baetidae. We have identified 10 specimens from the San Pedro River near Fort Huachuca. There are two known species in North America, *P. minutus* and *P. fleeki*, neither of which have been found in

Arizona. The taxonomy of our samples is being evaluated by experts, since our specimens are likely either a range extension of a species known only from North Carolina or a new species.

Figure 1.3 Specimens of the mayfly *Paracloedes* from the San Pedro River, Arizona, including images of diagnostic morphological features.

Patterns of biodiversity as a function of site characteristics. We used the dataset from Fort Huachuca to analyze the relationships between site-specific attributes and the biodiversity of aquatic invertebrates (Schriever et al. 2015). We first developed a trait database using over 80 publications from primary literature, databases and available specialist knowledge to define categorical trait states specific to the Southwest region. Each taxon was represented by a combination of traits, also known as its functional trait niche (FTN) (Poff et al. 2006). Functional trait diversity was represented by a species × trait matrix using 225 taxa for which we found complete trait information. We used 7 functional traits spanning a total of 30 modalities: body size, voltinism, respiration, functional feeding group, dispersal capability, diapause, and primary locomotion.

We calculated taxonomic richness, Shannon diversity, and evenness; and functional richness, functional diversity and functional evenness. Functional richness (FRic) measures the volume of functional space occupied by a community. FRic values are not constrained to the total number of trait modalities present in the species pool because they are calculated using the minimal convex hull that includes all species and quantifies the volume occupied by the community's traits (Villéger et al. 2008). We calculated functional diversity using the Shannon diversity index (H′) for each community with the species traits x species abundance matrix as well as for individual traits (species abundances within each trait state in each community sample). Functional evenness (FEve) describes the distribution of traits within a community (i.e., whether they are distributed evenly within occupied trait space) (Villéger et al. 2008). FEve ranges from 0 to 1, with low values representing unevenly distributed species traits within trait space (e.g., high density of species within a narrow range of trait space) and high values represent evenly distributed species traits throughout the functional trait space. FEve incorporates species abundances in calculation of the metric. FRic and FEve were calculated using the R-based FD package and the function dbFD (Laliberté and Legendre 2010).

We found a positive relationship between taxonomic diversity and functional diversity, providing evidence for higher functional redundancy at higher levels of diversity (Figure 1.4). Functional redundancy may offer resilience to environmental changes because of niche complementarity, as a greater range of traits available could allow more efficient resource use and provide insurance against changes in ecosystem function. Lower functional diversity implies lower ecological redundancy so that if stream hydrology were to transition from perennial to intermittent, unique traits could be lost that may lead to decreased productivity and disruption of ecosystem processes. For example, a single drying event could serve as a strong trait filter and cause the loss of drought-intolerant taxa and result in shorter food-chain length (Sabo et al. 2010). Thus, communities with lower functional richness and diversity may be susceptible to decreases in flow permanence because their communities have less redundancy and unutilized niche space. Climate change is expected to increase drought conditions by creating longer periods of low-flow conditions, resulting in intermittency of stream flow (Larned et al. 2010).
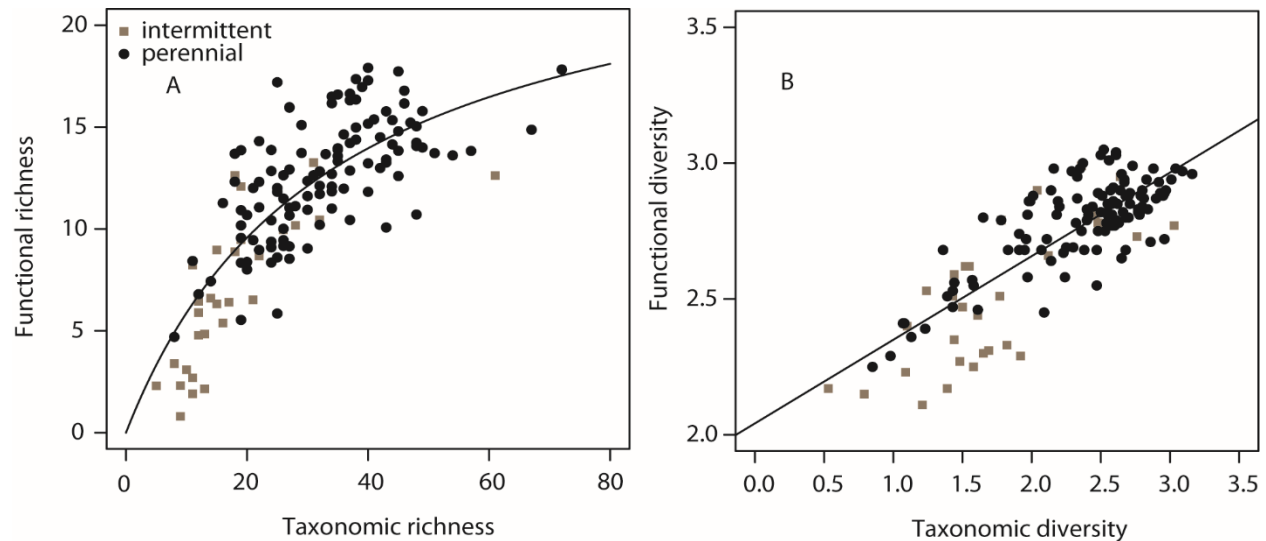
Figure 1.4 Aquatic invertebrate (A) functional richness and (B) functional diversity, Fort Huachuca, Arizona, USA. Sites are coded by whether they had flow during 100% of the sampling period (black dots - perennial) or not (gray squares - intermittent).

2 Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land streams

Synopsis: This chapter provides a general conceptual overview of how hydrology and drought events shape the aquatic invertebrate biodiversity in aridland ecosystems, such those encompassed by White Sands Missile Range, Fort Huachuca, and NAWS China Lake. It is focused primarily on expected and known empirical patterns, which we have used to guide the development of our niche-based and neutral biodiversity models.

2.1 Summary

1. Climate change is expected to intensify drought in many regions, but ecological impacts on stream communities are poorly understood. Many arid-land streams are characterized by predictable seasonal cycles of wetting and drying, to which species are adapted, but unpredictable supraseasonal droughts may constitute extreme events that challenge resident biota.

2. In this paper we synthesize research conducted in arid-land streams of the Madrean Sky Islands (MSI) in Arizona, USA, to evaluate the resistance and resilience of invertebrate communities to drying disturbances caused by normal seasonal drying and severe supraseasonal drought. We also highlight how spatial context (e.g. distance to perennial refuges) influences recovery patterns.

3. Invertebrate community structure changes predictably as habitat contraction progresses from loss of lateral connectivity to complete drying of MSI streams. When drying events are predictable (e.g. seasonal drying), post-drought community recovery is often rapid, since most MSI taxa possess life history traits conferring high resistance and/or resilience to stream drying.

4. Extreme supraseasonal droughts, in contrast, are causing unprecedented transitions from perennial to intermittent flow in some MSI streams. While species richness may recover quickly following this flow regime shift, marked turnover in community structure can occur and may delay or preclude recovery to pre-drought conditions. In such cases, shorter-lived (<1 yr), highly vagile, taxa replace those that are longer-lived ($\geq$ 1 yr) and have poor dispersal abilities. As habitat isolation increases, the potential for community recovery from extreme drought decreases.

5. Many MSI aquatic species are threatened by extreme drought. Extinctions of endemic aquatic species due to habitat drying have already been observed in nearby deserts. Further studies are urgently needed to identify drought-sensitive species and understand how the loss of such species may affect stream ecosystem functioning.

2.2 Introduction

Arid-land streams are characterized by harsh, but often predictable, cycles of flooding and drying (Lake, 2003). However, climate change and water withdrawals are altering flow regimes in these systems and may disrupt seasonal flow patterns, with uncertain impacts on resident biota (Barnett *et al*., 2008; Seager & Vecchi, 2010; Grantham *et al*., 2012; Ficklin, Stewart & Maurer, 2013). Climate models predict that the frequency, duration and severity of drought will increase across many arid and semi-arid regions (e.g. Seager *et al*., 2007). Because meteorological drought generally leads to hydrological drought (e.g. flow reduction or cessation: Boulton, 2003; Lake 2003), these more intense meteorological droughts will have major impacts on river flows. For instance, many stream basins in the western United States are expected to transition from a semi-arid to arid state by the 2080s, with summer flows declining by >45% (Ficklin *et al*., 2013). This intensification of drying disturbance presents significant challenges for stream biota adapted to predictable hydrology (Lake, 2003; Bêche *et al*., 2009; Ledger & Milner). Adaptations to seasonal drying (Boulton, 2003; Bogan & Lytle, 2007; Lytle, McMullen & Olden, 2008) may not confer stability to future events of unprecedented frequency, intensity or duration (Bogan and Lytle, 2011; Jaeger, Olden & Pelland, 2014).

Given the growing prevalence of drought in some regions, it is essential to understand how aquatic communities respond to stream drying and how they recover (or fail to recover) from these events. Boulton (2003) proposed a conceptual model of aquatic invertebrate community responses to drought in which periods of gradual biodiversity loss associated with declining water quantity and quality are punctuated by abrupt, significant losses of biodiversity caused by the loss of lateral, longitudinal, and vertical connectivity (also see Boulton & Lake, 2008). However, aquatic invertebrate species which experience regular drying disturbances, such as those in arid-land streams, are more likely to have life history adaptations that confer resistance and/or resilience to drought (Lytle & Poff, 2004). Evaluating the extent to which arid-land stream biota conform to Boulton's (2003) model would reveal whether their response to drying disturbance is typical or not and would also provide insight into their sensitivity to more extreme drought regimes.

While Boulton's (2003) conceptual model describes biodiversity loss during stream contraction and drying, it does not address post-event community recovery. Biotic recovery from stream drying partly depends on event predictability, and is often faster for annual seasonal drought than for aseasonal or unpredictable supraseasonal droughts (Gasith & Resh, 1999; Lake, 2003; Verkaik *et al*., 2013). Stream biota generally exhibit low resistance and variable resilience to supraseasonal drought (Lake, 2003). While definitions vary, we use the term resistance to describe the ability of individuals or communities to withstand a disturbance *in situ*, while the term resilience describes individuals' or communities' capacity to recolonize a site and reestablish populations or communities similar to those that were present before the disturbance. Our ability to interpret resistance or resilience at any given site requires knowledge of the disturbance history of the system, including the frequency and severity of antecedent droughts

(Lake, 2013). In addition to disturbance history, the spatial context in which drying disturbance occurs can shape post-disturbance recovery. Close proximity to drought refuges may facilitate recovery (Robson, Chester & Austin, 2011), whilst recovery in isolated habitats may take much longer (e.g. multiple years: Resh, 1992).

In this paper we synthesize research conducted in arid-land headwater streams of southeastern Arizona, USA, to evaluate ecological responses to seasonal versus supraseasonal drought. We report how aquatic invertebrate communities change as habitats contract and dry and describe the resistance and resilience mechanisms contributing to community recovery when habitats are rewetted. As seasonal drought in the study area often results in stream flow alteration that would be considered extreme in many regions (e.g. >95% habitat contraction and/or complete flow cessation: Bogan & Lytle, 2007), we first describe the impacts of these harsh, but predictable, seasonal droughts. We then consider the effects of unpredictable supraseasonal droughts which produce unusually intense drying events that extend into one or more wet seasons. We also discuss the spatial factors that constrain community recovery following these different types of droughts. We use these findings to adapt the conceptual model developed by Boulton (2003), and include potential post-drought recovery trajectories to explore whether extreme drought events alter even the most drought-adapted arid-land stream communities.

2.3   Study region and streams
The work we describe here was conducted in headwater streams of the Madrean Sky Islands (MSI). The MSI region encompasses a series of >30 semi-arid mountain ranges (2000-3300 m) isolated from one another by arid, lowland desert (800-1200 m). Stream networks in the region are not connected by continuous flow, but rather exist as a series of isolated perennial or intermittent headwater reaches, with long ephemeral reaches between perennial habitats (Bogan, Boersma & Lytle, 2013; Stromberg *et al*., 2013). While some aquatic invertebrates (e.g. Dytiscidae: Coleoptera) in the region readily disperse among these isolated aquatic habitats (Bogan & Boersma, 2012), genetic analyses of others (e.g. Hemiptera: Belostomatidae) indicate that dispersal across arid uplands is very limited (Finn, Blouin & Lytle, 2007; Phillipsen & Lytle, 2013).

The flow regimes of MSI streams are determined by a bimodal precipitation cycle that consists of intense, highly localized, summer monsoons (Jul-Aug) and less intense, more widespread, winter rains (Nov-Mar). Summer monsoons cause destructive flash floods in MSI streams (Lytle, 2000) but generally do not increase flow for more than a few days following storms (Paulson *et al*., 1991). Winter precipitation, in contrast, can raise groundwater levels across the region and result in widespread flow in intermittent reaches and increased baseflow in perennial reaches (Bogan & Lytle, 2007; Bogan *et al*., 2013a). While some MSI streams flow all year, most fragment to perennial pools or dry completely during dry seasons, especially in early summer (April-June) when wetted habitat area can contract by >95% (Figure 2.1, arrows; Bogan & Lytle, 2007). Many MSI streams with intermittent flow will dry completely during early summer, and

may be dry for >9 months each year (Bogan *et al.*, 2013a). Ephemeral streams in the region generally flow for only a few hours or days following heavy precipitation (Jaeger & Olden, 2012), and were not sampled in the studies reviewed here. In addition to seasonal variation in precipitation and flow, interannual variation in these factors is also quite high. El Niño events (e.g. 2005, 2010, Figure 2.1) bring abundant winter rains which result in higher flows in perennial reaches and widespread activation of intermittent reaches, while La Niña events (e.g. 2009) may bring so little rain that no winter flow occurs.
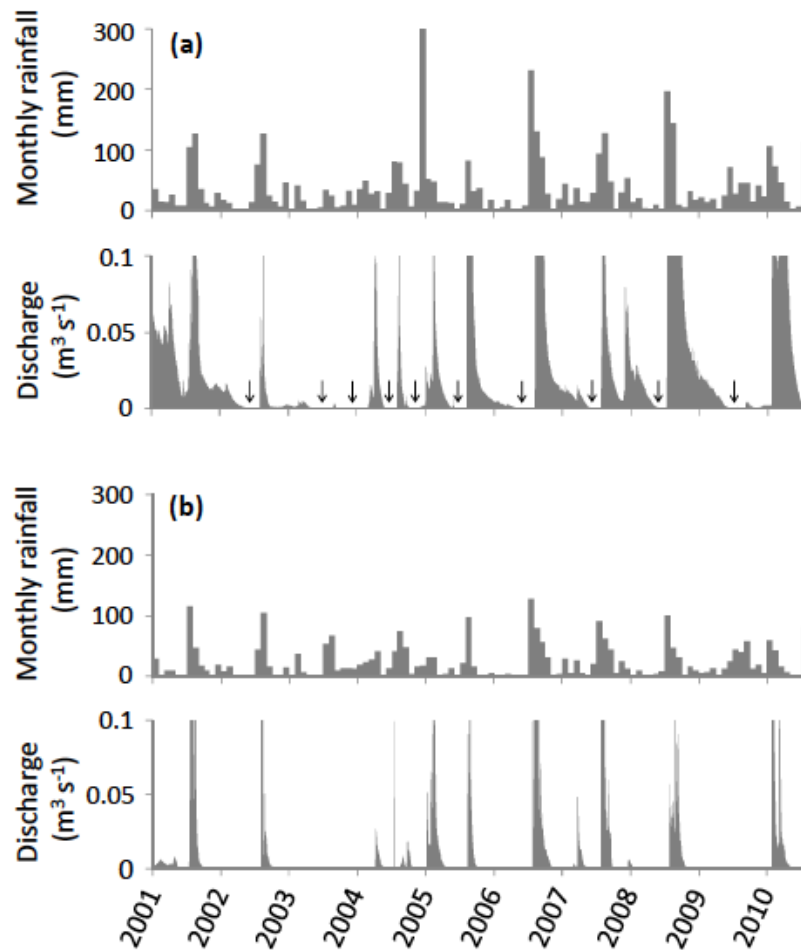
Figure 2.1 Examples of the high seasonal and interannual variability in monthly rainfall (mm) and daily mean stream discharge ($m^3 s-1$) in Madrean Sky Island streams, including (a) a perennial stream (Garden Canyon, AZ) where pools remain even when flow ceases during seasonal drought (indicated by arrows) and (b) an intermittent stream (Banning Creek, AZ) where flow occurs only during rainy seasons and the stream is completely dry for months (or years) between rainy seasons. Data are from United States Geological Survey flow gauges and peak discharges are truncated to facilitate display of dry season differences.

Despite this high seasonal and interannual flow variability and the limited amount of aquatic habitat in this arid region, the MSI harbors a diverse aquatic invertebrate fauna. To date, we have

recorded over 400 aquatic invertebrate taxa from the MSI (Bogan, 2012; Bogan *et al.* 2013b; Bogan *et al.*, 2013c). This high diversity is due in part to the overlapping biogeographic distribution of Nearctic and Neotropica faunas, and the large number of regional endemics (Warshall, 1994; Bogan & Lytle, 2007; Bogan et al. 2013b). MSI streams are ideal model systems to explore aquatic community responses to drought because they are highly diverse, tractable (i.e. small habitats simplify sampling and species detection), and can be replicated experimentally (i.e. via mesocosms which mimic dry season pools). Resident biota regularly experience harsh seasonal drought conditions and are generally regarded as being relatively resistant and/or resilient to predictable drying disturbances. However, it is less clear whether species with adaptations to regular drying events will persist through extreme droughts with no historical analogue (Leigh 2013; Jaeger at al. 2014).

2.4   Changes in species richness and community composition along a drying gradient

Loss of lateral connectivity. Loss of lateral connectivity of surface water occurs at the earliest stages of drought in streams, when formerly submerged riparian littoral areas dry (Figure 2.2: threshold A). In many regions, this first transition represents an important loss of unique microhabitat, such as beds of aquatic plants or the submerged roots of riparian trees (Boulton, 2003). Arid-land streams, however, are rarely connected laterally to riparian corridors. Rather, many of these streams are in a state of either expansion or contraction (Stanley, Fisher & Grimm, 1997) and connection to lateral margins of the stream channel occurs only briefly. Thus, in most arid-land streams, it is unlikely that many species specialize in these ephemeral marginal habitats. However, a very small number of MSI streams are spring-fed and have nearly constant flow, including stream habitats known regionally as ciénegas (Hendrickson & Minckley, 1985) and desert oases (Felger, 1999). These spring-fed habitats support several species that are rare or absent in runoff-fed streams, including caddisflies that feed on aquatic vegetation (e.g., Hydroptilidae: *Oxyethira*) or freshwater sponges (Spongillidae) that encrust on submerged roots and support regionally rare populations of the spongillafly *Climacia chapini* (Bogan et al., 2014). Thus, we would expect the loss of a small number of specialized species if drought or water withdrawals were to cause flow in these spring-fed habitats were to decline and leave lateral stream margins dry (Figure 2.2: threshold A).
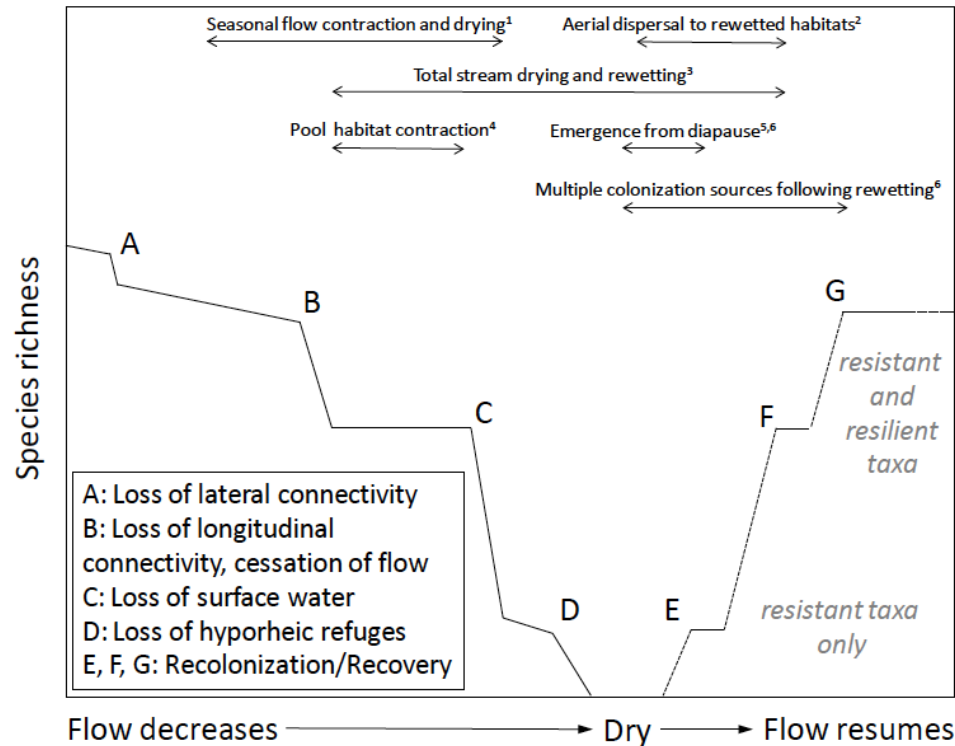
Figure 2.2 Changes in aquatic invertebrate species richness in Madrean Sky Island streams as flow decreases due to drought conditions (solid line) and potential recovery trajectories (dashed line) following flow resumption [adapted from Boulton (2003)]. A – D: thresholds during drying when species richness declines rapidly due to macrohabitat loss. E: recovery by drought-resistant taxa only. F: recovery of species richness via aerial recolonization of resilient taxa. G: full recovery of species richness via multiple resistance and resilience (instream and overland) pathways. Arrows at the top of the figure indicate processes contributing to species loss during drying and recovery, and describe the time frames in which they are important. Superscripts reference studies quantifying the relationship between species richness and drying and rewetting events: [1]Bogan & Lytle, 2007; [2]Bogan & Boersma, 2012; [3]Bogan & Lytle, 2011; [4]Boersma et al., 2014; [5]Bogan et al., 2013a; [6]Bogan, 2012.

Flow reduction and loss of longitudinal connectivity. Streams that maintain any year-round flow are uncommon in the MSI. Most streams in the region have only intermittent or ephemeral flow, though perennial pools may persist (Bogan & Lytle, 2007; Bogan *et al*. 2013a). Streams with perennial flow support a number of taxa that are rare or absent in streams with temporary flow, including riffle beetles (Elmidae), water penny beetles (Psephenidae), crawling water bugs (Naucoridae), and several families of stoneflies (Perlidae, Perlodidae and Chloroperlidae). A slight decline in the richness of assemblages is evident along a gradient of perennially flowing streams in the MSI (Figure 2.2: between thresholds A and B), from larger streams that maintain strong flow during seasonal drought to smaller streams that maintain only trickles of flow during the dry season (Bogan, 2012; M.T. Bogan, unpublished data). Some taxa (e.g. Elmidae: *Macrelmis*; Psephenidae: *Psephenus*; Perlidae: *Anacroneuria*, *Hesperoperla*) are found only in larger streams that are less prone to seasonal flow declines, while others (e.g. Elmidae: *Zaitzevia*,

Microcylloepus; Naucoridae: *Ambrysus*) are found across a range of flow types, including in streams where perennial riffles contract to small trickles (<4L/min) during seasonal drought.

As drought conditions persist for several months, intermittently flowing streams in the MSI cease flowing entirely and only isolated perennial pools remain (Figure 2.1). Boulton (2003) noted that this transition would likely be accompanied by a large loss of lotic species, with only lentic taxa remaining in stagnant water, a pattern observed in other arid-land stream systems (Stanley *et al*., 1994; Leigh 2013). In MSI streams, most lotic taxa disappear locally as longitudinal connectivity is lost, including stoneflies (e.g. Capniidae, Nemouridae), mayflies (e.g. Baetidae: *Baetis*) and caddisflies (e.g. Hydropsychidae), leaving only a tolerant subset of the year-round beetle (e.g. Dytiscidae: *Rhantus*, *Stictotarsus*), true bug (e.g. Belostomatidae: *Abedus*), caddisfly (e.g. Calamoceratidae: *Phylloicus*) and true fly taxa (e.g. Chironomidae, Stratiomyidae).The decline in species richness in these perennial pools due to flow cessation is only transient, however, as numerous species in several beetle and true bug families (e.g. Notonectidae, Corixidae, Hydrophilidae) soon colonize the pools. This seasonal drought-induced 'time-sharing' of stream habitats between the lotic Nearctic stonefly, mayfly, and caddisfly taxa and lentic Neotropical beetle and true bug taxa occurs across the region (Bogan & Lytle, 2007; Bogan, 2012), provided that off-season refuges are available to serve as colonization sources (see below). While the drying disturbance of seasonal drought does result in the local loss of many lotic species, these events actually increase the total number of species found at a site through time by opening up stream habitat to different taxa during the dry season (Bogan and Lytle 2007). This predictable seasonal drying disturbance thus enables more aquatic invertebrate species to occupy a given MSI stream than would be found in the absence of seasonal drought.

Declining water levels in remnant pools. As water evaporates and groundwater inputs decline during seasonal drought, water levels in remnant pools decline and water temperature and conductivity increases whilst dissolved oxygen concentrations decrease (Lake 2003). Whether such intensifying abiotic conditions reduce taxonomic diversity depends on the local history of drought and the extent to which aquatic organisms at a given site possess traits to withstand drying (Lake, 2003; Lytle & Poff, 2004). Where local taxa are adapted to predictable seasonal droughts, drying may not significantly reduce diversity until all surface water is lost. Pool drying is a complex process that can modify many biotic and abiotic processes (Boulton, 2003), and experimental manipulations are necessary to disentangle various potential mechanisms.

To experimentally test the relationship between declining pool volume and MSI aquatic invertebrate community structure during seasonal drought, Boersma *et al*. (2014) conducted a mesocosm study during the dry season using aquatic invertebrates collected from three MSI streams. They created mild, moderate and severe pool contraction treatments (water depths of 10, 7 and 1cm, respectively) and restricted both emigration from and immigration to mesocosms to isolate community resistance to drying from resilience following drying. At the end of the six-week experiment, severe drying increased conductivity and temperature above that in the other treatments, but community structure was not affected. Boersma *et al*. (2014) also calculated the

functional diversity of traits associated with respiration, diapause, body size and functional feeding role and again found no treatment effect. This experiment revealed the high resistance of dry season taxa throughout the drying process and suggests that MSI stream pool taxa are well-adapted to harsh abiotic conditions, excepting complete drying.

Loss of vertical connectivity (complete stream drying). Complete stream drying occurs in temporary streams during typical drought seasons (Figure 2.1; Bogan *et al.*, 2013a), but may also occur in normally perennial pools during unusually intense or prolonged droughts (Bogan & Lytle, 2011). This loss of vertical connectivity to groundwater causes a drastic reduction in invertebrate richness, including the local extirpation of lentic fauna. Even highly resistant beetles, true bugs and true flies tolerant of marked reductions in water depth cannot withstand complete stream drying (Figure 2.2: threshold C), and many species use increasing water temperatures and conductivity as cues to aerially disperse from drying pools in search of perennial habitats (Velasco & Millan, 1998). Other taxa use positive rheotaxis to move toward perennial reaches during drying events (Lytle *et al*. 2008). In the MSI, flightless species (e.g. Belostomatidae: *Abedus herberti*) may abandon dried pools and crawl along the dry stream channel in search of perennial water (Boersma & Lytle, *in press*). By contrast, many poor dispersers remain within the drying habitat and may seek refuge under damp substrata (e.g. *A. herberti*; Dytiscidae: *Agabus*; M.T. Bogan & D.A. Lytle, personal observations). Refuge-seeking behavior has also been reported in nearby Sonoran Desert streams (Stanley *et al*., 1994; Shepard, 2011). These damp refuges are transient however and generally do not last longer than a week or two, after which time pool inhabitants have either dispersed aerially, sought refuge deeper in the hyporheic zone, or perished (Stanley *et al*., 1994).

Loss of wetted hyporheic habitats. There is some evidence that invertebrates can avoid dry surface conditions by migrating to wet hyporheic sediments (Stubbington, 2012), but during intense droughts even these subsurface refuges can desiccate, impacting interstitial biota. Research on the hyporheos of MSI streams is lacking, but in nearby Sonoran Desert streams, mature biting midge larvae (Ceratopogonidae: *Probezzia*) appear almost immediately when surface flows resume, suggesting they use the hyporheic zone as a refuge from surface drying (Stanley et al., 1994). Horsefly larvae (Tabanidae: *Tabanus*) can also diapause in these hyporheic habitats to avoid dry periods (Gray, 1981). Surface-dwelling invertebrates (e.g., *Probezzia*, *Tabanus*) are typically detected in the shallower sediments (<50 cm depth), suggesting they may be vulnerable to hyporheic drying as interstitial water levels decline (Figure 2.2: between thresholds C and D). Surveys in Sonoran Desert streams found many obligate hyporheic invertebrates (10-50 taxa, mainly copepods, amphipods and mites) in deep sediments (up to 100 cm depth, Boulton, Valett & Fisher, 1992; Clinton, Grimm & Fisher, 1996). These taxa can migrate even further (>100cm) to escape declining groundwater levels (Clinton *et al*., 1996), but may be threatened where groundwater recedes to great depth during extreme drought (Figure 2.2: threshold D). Consistent with this, arid-land streams that dry to bedrock contain less diverse hyporheic communities than those that retain some water at depth, suggesting that many obligate

hyporheic taxa lack desiccation-resistant stages (Cooling & Boulton, 1993; Boulton & Stanley, 1995). In the case of complete hyporheic drying, only taxa with an anhydrobiotic resting stage (e.g., diapausing eggs or larvae) persist.

2.5 Resistance and resilience to seasonal and supraseasonal drought: recovery following rewetting

The wet/dry seasonal and interannual cycles that characterize the MSI region eventually return water to dry streams, even if only briefly (Figure 2.1), providing an opportunity for aquatic community recovery (Figure 2.2: thresholds E through G). Following drought, local species richness and community composition depend on two primary factors: (1) the severity of the drying disturbance (i.e. is drought mild or extreme?) and (2) the geographic context of the recovery process (i.e. are colonist sources near or far?) (Robson *et al*., 2011). The local history of drought frequency, duration and magnitude may also shape aquatic invertebrate responses to future disturbances. For example, a short-duration (e.g. 2 month) drying event is likely to be of little biological significance in an intermittent stream dominated by species with life history adaptations to drought, but may well represent an extreme disturbance in a perennial stream with no history of drying.

Recovery via resistance mechanisms. Few surface-dwelling aquatic invertebrates are truly resistant to complete drying of MSI streams but there are a small number of specialized stoneflies (Capniidae), midges (Chironomidae), blackflies (Simuliidae) and dobsonflies (Corydalidae) that have egg or larval diapause stages that can withstand long dry periods (>9 months; Bogan & Lytle, 2007; Bogan, 2012; Bogan *et al*., 2013a). These taxa are found almost exclusively in intermittent streams, including streams that are dry for a year or longer (Fig. 1b), and are seldom encountered in reaches with perennial flow (Bogan *et al*., 2013a). While taxonomic richness in these highly intermittent streams may only reach 10-20 species following rewetting (Figure 2.2: threshold E), recovery occurs rapidly. Many resistant taxa reappear within 2-3 days of flow resumption (Bogan, 2012), and within 8-10 weeks invertebrate densities in intermittent reaches are often equal to those in perennial reaches (Bogan *et al*., 2013a). As most MSI intermittent streams are geographically isolated (>10 km) from perennial reaches and flow for only 10-12 weeks at a time, the stream fauna typically exhibits low diversity, with further community development curtailed by stream re-drying.

Recovery via resilience mechanisms. Few MSI aquatic invertebrate species are resistant to drought but many use aerial dispersal as a resilience mechanism. The predaceous diving beetle *Agabus* (Dytiscidae) is often one of the first predators to aerially colonize intermittent streams on rewetting (Bogan, 2012). The beetles use these habitats for breeding, and both larvae and adults consume the drought-resistant stoneflies, midges and blackflies that are abundant in the early stages of flow resumption (Bogan *et al*., 2013a). *Agabus* was the first beetle colonist in a Sonoran Desert stream during the winter flow period, where they completed their life cycle in 4-8 weeks (Gray, 1981). Adult dytiscids are strong aerial dispersers (Bogan & Boersma, 2012) and

can detect polarized light reflecting from the water surface (Schwind, 1991). However, many other aerially-dispersing species fail to locate isolated intermittent sites during the short (10-12 week) winter hydroperiod (Figure 2.1b), and are restricted to intermittent streams with more persistent flow. For example, aerial colonization of an isolated (2 km to refuges) intermittent stream with a relatively long (20-week) hydroperiod took 16 weeks for some taxa (e.g., Lestidae: *Archilestes*; Hydroptilidae: *Hydroptila*; Psychodidae: *Maurina*) (M.T. Bogan, unpublished data).

Monsoon rainfall during the summer triggers the aerial dispersal of aquatic invertebrates among MSI freshwater habitats, including from perennial refuges to newly rewetted streams (Bogan, 2012). In arid regions, the increased humidity associated with rainfall events may prolong survival of aquatic species as they disperse. In a colonization experiment along two MSI streams, the quantity of monsoon rainfall explained 75% of the variation in aerial colonization of mesocosms near streams (Bogan & Boersma, 2012). In the same experiments, 66 invertebrate taxa (one-third of the local species pool) colonized mesocosms in six weeks. A related recolonization study of isolated (10 km from the nearest perennial stream) monsoon-refilled stream pools recorded 40 aerially colonizing taxa over three months (Bogan & Lytle, 2011). In fact, the vast majority of the drought tolerant taxa that dominate perennial stream pools in the pre-monsoon dry season are strong aerial dispersers (Boersma *et al.*, 2014) that can rapidly colonize rewetted sites (Figure 2.2: threshold F).

 The most complete recovery observed in MSI streams following seasonal or supraseasonal drought (Figure 2.2: threshold G) occurs in sites that regain flow for at least 4-5 months and are near, and perhaps directly downstream of, perennial refuges. In high elevation (2800-3300 m) MSI mountain ranges, headwater seeps and springs constitute year-round cool water refuges from which Nearctic fauna disperse to repopulate downstream reaches in winter (Bogan & Lytle, 2007). This seasonal pattern of recovery of Nearctic-derived assemblages from refugia has been widely observed across the MSI (Bogan & Lytle, 2007; Bogan, 2012). Invertebrates recolonize rewatered habitats by several routes, notably drift from upstream sources, aerial dispersal (e.g. Dytiscidae: *Rhantus*, *Stictotarsus*), redistribution from instream refugia (e.g. Limnephilidae: *Hesperophylax*; Siphlonuridae: *Siphlonurus*) or via diapause (e.g. Blephariceridae: *Agathon*; Capniidae: *Eucapnopsis*). Frequently, robust recovery from drought in MSI streams is underlain by a combination of resilience and resistance mechanisms (Figure 2.2: threshold G).

Extreme supraseasonal drought and lack of recovery to pre-drought conditions. The recovery trajectories described thus far have all been observed in streams experiencing drought and drying disturbances that are within the normal range of historical disturbance events for those systems. For example, resistance-dominated recovery patterns occur in intermittent streams which dry predictably each year and are rewetted only for short time periods (e.g. 10 weeks). Resilience-dominated recovery of Nearctic-derived stonefly, mayfly and caddisfly assemblages in other MSI streams occurs when flow returns after predictable dry season contraction to isolated pools and other refuges (e.g. headwater springs). However, these observations may not adequately predict recovery patterns in streams that experience extreme supraseasonal droughts.

Unprecedented drying disturbances, such as transitions from perennial to intermittent flow, may generate novel community trajectories (e.g. Bêche et al., 2009; Sponseller et al., 2010; Bogan & Lytle, 2011).

In the MSI, a recent 6-year supraseasonal drought (1999-2005) was the most intense documented in the historical record (Seager, 2007) and resulted in the lowest streamflows ever recorded in the region (Phillips & Thomas, 2005). This extreme drought resulted in the loss of vertical connectivity and the complete drying of all surface habitats at one MSI stream, French Joe Canyon, as documented during an 8-year observational study (Bogan & Lytle, 2011). Prior to this, genetic, geomorphic and anecdotal evidence all suggest that flow at French Joe had been perennial for hundreds of years or longer. Nevertheless, following the supraseasonal drought, French Joe transitioned to intermittent flow (in 2005), drying and rewetting a further 2-3 times over the next four years.

The unprecedented flow regime shift at French Joe had surprisingly little effect on aquatic invertebrate taxon richness, but significantly altered community composition (Bogan & Lytle, 2011). Within three months of flow resumption in 2005, richness equalled that of pre-drying conditions, although the identity of those taxa changed dramatically. Six species were extirpated by the initial drying event at French Joe, including the flightless top predator (Belostomatidae: *Abedus herberti*) and the largest shredder (Calmoceratidae: *Phylloicus mexicanus*). These dispersal-limited species failed to recolonize in the ensuing four years, likely because French Joe is nearly 10 km from the nearest perennial stream habitat. The pre-drying community was dominated by relatively large, long-lived and sedentary taxa whereas the post-drying taxa were smaller, shorter-lived, and highly vagile, including strong aerial dispersers that readily colonize newly wetted habitats (Bogan & Boersma, 2012). The composition of French Joe Canyon's aquatic invertebrate community has not returned to its pre-drying state, nearly 9 years after transitioning to intermittent flow (M.T. Bogan, unpublished data). Since all evidence suggests that French Joe had not experienced complete drying prior to 2005, resident taxa did not possess resistance traits (e.g. drought-resistant diapause stages) such as those observed in MSI streams with a historical context of predictable intermittency (Bogan *et al*., 2013a). Hence, the lack of post-drying recovery in community composition at French Joe resulted from a combination of historical context, drought severity and the site's geographic location.

Conceptual model of the impacts of drought severity and habitat isolation on local species richness. Our research in the MSI region suggests aquatic invertebrate community responses to, and recovery from, drought varies with drought severity and stream geographic isolation (Figure 2.3). Here, we use species richness as a descriptor of community recovery to illustrate our model because the metric responds fairly uniformly to drying disturbance across geographic regions (Datry *et al*., 2014) and effects of isolation are well-documented elsewhere (e.g. MacArthur & Wilson, 1967). Our observations suggest invertebrate species richness is highest in streams with mild and predictable seasonal drought (e.g. flow cessation for 4-6 mo/yr) where perennial refuges are nearby to serve as a source of colonists (Point A). At such sites, 'time-sharing'

occurs, with lotic taxa exploiting running water habitats in the wet season and lentic taxa using pools in the dry season. Where seasonal drought does not occur, higher flows would exclude some lentic taxa thus reducing species diversity from its peak (left of point A). Where streams are most isolated, local species richness is relatively low, reflecting stochastic extirpations of fauna with weak dispersal abilities (Point B). Intermediate drought severity and isolation also constrain local species richness as some weak dispersers and drought-sensitive taxa are absent (Point C). Streams that experience severe drought are generally dominated by a few resistant taxa. However, where these streams are close to perennial refuges, then some resilient taxa may also colonize, thereby increasing diversity over that of highly isolated streams (Point D). Sites with both high isolation and high drought severity often support very few, highly resistant, species (Point E).

A: Predictable, mild seasonal drought and low isolation-- *lotic and lentic taxa 'time-share' between wet and dry season*

B: Low drought severity, high isolation-- *weak dispersers experience stochastic extirpations*

C: Moderate drought severity and isolation-- *some sensitive taxa and weak dispersers are lost*

D: High drought severity, low isolation-- *resistant taxa and colonists from nearby refuges*

E: Severe drought and isolation-- *only the most resistant taxa remain*

Figure 2.3 A conceptual model illustrating potential interactive effects of drought severity (defined here as a combination of drying intensity and duration) and habitat isolation (distance to nearest perennial refuge) on aquatic invertebrate species richness in streams. This model was constructed with a combination of ecological theory (e.g. theory of island biogeography) and observations from the Madrean Sky Island stream studies reviewed here. A: mild drought disturbance (e.g. brief seasonal drying) increases the overall richness of a given site by allowing lentic taxa to colonize the stream for part of the year. B-D: high drought severity or isolation, or a combination of moderate drought severity and isolation, act as abiotic filters to reduce richness. E: only a few highly resistant or resilient taxa can persist in highly isolated sites that also experience high drought severity.

2.6 Conclusion

Over the past 15 years, southwestern North America has experienced extreme droughts that equal or exceed any documented in the historical record (Seager, 2007). Although these recent droughts are slightly less intense than those of the medieval warm period from AD 900-1200, the record high temperatures of the 20th and 21st centuries may be amplifying their hydrological effects (Woodhouse *et al*., 2010). In addition to these patterns of increasing temperature and drought severity, anthropogenic water withdrawal across southwestern North America has further decreased stream flow in many basins (Deacon *et al*., 2007; Barnett *et al*., 2008; Grantham *et al*., 2012). Many arid-land streams are characterized by seasonal and interannual periods of drought, but decreasing rainfall, rising temperatures and growing water withdrawals are intensifying these historical disturbance regimes. This combination of factors is causing some MSI streams to transition from perennial to intermittent flow. When these extreme drying events and flow regime transitions occur in isolated streams, resident taxa adapted to perennial flow exhibit very low resistance and variable resilience to these unprecedented disturbances. Numerically, species richness may recover in these streams, but long-lived taxa and weak dispersers are replaced by more vagile or short-lived taxa. These 'replacement' taxa may not be functionally equivalent to the extirpated taxa, especially since drought-sensitive taxa in the MSI include the largest predators and shredders in the region.

These observations highlight the need for more species-specific dispersal data, and a greater understanding of the spatial context in which a disturbance occurs, in order to adequately predict community responses to climate change (Travis *et al*., 2013). If extreme supraseasonal droughts occur more frequently, as is predicted for southwestern North America (Seager *et al*., 2007), then widespread transitions from perennial to intermittent flow and increased isolation of remaining perennial habitats could eventually lead to species-level extinctions. Unprecedented stream drying may also have cascading effects on the biodiversity of riparian areas (McCluney & Sabo, 2012).

MSI streams support numerous invertebrate species with limited distributions, including those only recently known to science (e.g. Ruiter, 2011) or endemic to a single mountain range or spring (e.g. Smith & Cook, 2006). Drought and water withdrawals have already caused the extinctions of regionally endemic springsnail species in the nearby Chihuahuan Desert (Hershler, Liu & Landye, 2011). In the MSI, invertebrate taxa with weak dispersal abilities (e.g. *Abedus herberti*) or those dependent upon the few remaining streams with strong, cool, year-round flow (e.g. *Hesperoperla*) may be useful as sentinel species of climate change, and their populations should be monitored.

While short-term studies can elucidate the impacts of and recovery from seasonal disturbances, only long-term studies can reveal the unique impacts of supraseasonal drought (cf. Jackson & Fureder, 2006). Recent long-term studies of streams in arid and semi-arid regions of North America (Bêche et al., 2009; Sponseller et al., 2010), the Mediterranean (Pace, Bonada & Prat,

2013) and Australia (Chessman, 2009) have advanced understanding of both general and system-specific responses of aquatic communities to supraseasonal drought. Additionally, well-designed mesocosm experiments can simulate the effects of unprecedented drying disturbances. Recent mesocosm studies along British streams showed that invertebrate communities were resilient to stream drying occurring at relatively low frequency (quarterly) but impoverished when these events occurred more often (monthly), despite the close proximity of potential colonists (Ledger *et al.*, 2013). Although logistically challenging, long-term mesocosm manipulations (e.g. Chase, 2007) may be a valuable way to examine the mechanisms underpinning responses to changing flow regimes.

We hope that our regional synthesis inspires further research on drought impacts in stream ecosystems. Specifically, we suggest that the following topics would be fruitful avenues of research: (1) measuring species-specific overland dispersal capabilities to predict how species will respond to increased habitat isolation in drought-affected streams, (2) conducting long-term mesocosm studies that manipulate both drought intensity and colonization potential, (3) analyzing the biological traits of species experiencing extreme drought to link changes in aquatic communities to ecosystem functioning (e.g. impacts of shredder extirpations), (4) examining how the rate of stream drying and the manner of flow resumption affect biotic responses to drought, and (5) quantifying the predictability and intensity of drought events across multiple regions to determine how these factors shape biodiversity and community composition. The latter suggestion would facilitate comparisons across biotic regions (mesic and xeric) and allow for quantitative global meta-analyses of drought impacts, as have been conducted for flood disturbance (e.g. McMullen & Lytle, 2012). Knowledge gained from a diversity of regions will be essential to understanding how stream ecosystems will respond to future extreme drought events.

2.7   Acknowledgements

3 Linking multidimensional functional diversity to quantitative methods: A graphical hypothesis-evaluation framework

Synopsis: This chapter introduces the concepts of trait space and the analysis of functional, as opposed to taxonomic, diversity. Analysis of species traits such as dispersal ability, hydroperiod requirements, generation time, and body size is becoming a powerful tool for niche-based modeling, since it allows us to generalize findings to regions that have functionally-similar but taxonomically-distinct species pools. The chapter builds a conceptual framework for traits analysis, and contributes novel statistics for testing among competing hypotheses.

3.1 Abstract

Functional trait analysis is an appealing approach to study differences among biological communities because traits determine species' responses to the environment and their impacts on ecosystem functioning. Despite a rapidly expanding quantitative literature, it remains challenging to conceptualize concurrent changes in multiple trait dimensions ("trait space") and select quantitative functional diversity methods to test hypotheses *a priori* to analysis. To address this need, we present a widely applicable framework for visualizing ecological phenomena in trait space to guide the selection, application, and interpretation of quantitative functional diversity methods. We describe five hypotheses that represent general patterns of responses to disturbance in functional community ecology and then apply a formal decision process to determine appropriate quantitative methods to test ecological hypotheses. As a part of this process, we devise a new statistical approach to test for functional turnover among communities. Our combination of hypotheses and metrics can be applied broadly to address ecological questions across a range of systems and study designs. We illustrate the framework with a case study of disturbance in freshwater communities. This hypothesis-driven approach will increase the rigor and transparency of applied functional trait studies.

3.2 Introduction

For over a century ecologists have sought to explain observed differences among biological communities. As a result, many approaches have been developed to simplify species assemblages into quantifiable units using indices such as species richness, diversity and evenness (e.g., MacArthur 1965, Whittaker 1972, Hill 1973). Recently, trait-based methods have emerged as an appealing way to quantify and explain community differences (Weiher and Keddy 1995, Petchey and Gaston 2002, McGill et al. 2006, Suding et al. 2008). Functional traits are an useful currency with which to understand community dynamics because they can determine how species respond to the environment ("response traits") and affect ecosystem functioning ("effect traits"; Naeem and Wright 2003). Further, communities that have no species in common will share functional traits (e.g., body size), and trait values can be compared among individuals within and between communities. Thus, trait analyses may highlight patterns across ecosystems that are not apparent in taxonomic analyses (e.g., Lavorel et al. 2013, Parravicini et al. 2014).

The sheer quantity of recent functional diversity (FD) studies indicates that a functional approach to ecology is an attractive means to detect similarities or differences in community assembly patterns.

Many approaches have been developed to quantify the composition of functional trait states within and among communities ("multivariate trait composition"). Some of these methods, such as multivariate ordination, account for trait non-independence (Petchey and Gaston 2006) and the potential for suites of traits to respond in concert to the environment (Mouchet et al. 2010). Currently, there are over 20 metrics to measure various facets of multivariate trait composition, and a large body of reviews, frameworks, and primers attempting to guide ecologists through this growing analytical complexity (Petchey et al. 2004, Petchey and Gaston 2006, Mouchet et al. 2010, Cadotte et al. 2011, Schleuter et al. 2011, Kleyer et al. 2012, de Bello et al. 2013, Mason et al. 2013, Mouillot et al. 2013b, Spasojevic et al. 2014). This diversity of approaches is inspiring; however, it requires informed metric selection that is appropriate to address specific research questions.

Researchers have begun to apply these quantitative FD approaches to rigorously test ecological hypotheses. For instance, Mason and colleagues (2012) applied a functional approach to examine coexistence mechanisms in woody plant communities through convergence and divergence in resource-use traits relative to soil fertility. Similarly, Laliberté and colleagues (2013) examined convergence in plant functional traits to test the influence of environmental filtering and niche overlap on plant community composition along gradients of primary productivity and grazing disturbance. These two studies are exemplary because they explicitly outlined a hypothesis of functional difference (trait convergence/divergence) and selected a quantitative FD metric from the literature (functional richness; Mason et al. 2005) to test the hypothesis and interpret results. However, FD may differ among communities in a variety of ways, beyond convergence and divergence, and it is not always clear which differences in the structure of trait space are most relevant for testing other ecological hypothesis about functional difference.

The complexity of combining information on multiple traits for multiple taxa makes it challenging to formulate ecologically informed, multivariate hypotheses and then use these hypotheses to select appropriate quantitative methods in a rigorous and transparent manner. An intuitive framework is needed to guide hypothesis-driven selection of quantitative FD methods. Then, the hypotheses of interest can determine appropriate quantitative analyses to test them, rather than selecting metrics post-hoc or adopting methods designed for other applications without thorough assessment. A hypothesis-driven approach can also determine when metrics do not yet exist for detecting possible FD responses of interest, and therefore motivate development of new quantitative approaches. This way, researchers can ensure that ecological questions drive methodological development instead of vice versa.

We present an intuitive framework that outlines a broad set of ecological hypotheses about functional differences among communities and provides direct ways to test these hypotheses.

This framework uses graphical hypotheses of functional responses to disturbance to guide the selection, application, and interpretation of FD methods. We highlight the need for ecologically motivated metric development and selection by describing a novel quantitative metric that quantifies functional turnover between communities. We demonstrate the framework with a case study from an aquatic ecosystem.

3.3   A graphical hypothesis framework

It is widely appreciated that multidimensional trait space can be a useful foundation on which to build research questions and generate hypotheses (Rosenfeld 2002). The functional trait composition of a community can be visualized with species' combinations of trait states as points in a Euclidean functional "trait space" (Figure 3.1). This trait space can be constructed by two or more traits to generate an n-dimensional space. Ordination techniques such as non-metric multidimensional scaling or principal components analysis can be applied to create a reduced-dimensionality approximation of the distances between objects in the original n-dimensional trait space. The position of each point on the ordination is determined by a specific combination of trait values (hereafter "trait combination," as per De Bello et al. 2005), and therefore points that are closer together represent species with similar trait composition. If species abundance information is available, the number of individuals possessing a particular trait combination can be indicated by point size (Rosenfeld 2002, Mouillot et al. 2013b). This way, trait information on many species can be combined visually to characterize the multivariate trait composition of entire communities (e.g., Mouchet et al. 2010, de Bello et al. 2013b, Mouillot et al. 2013b).
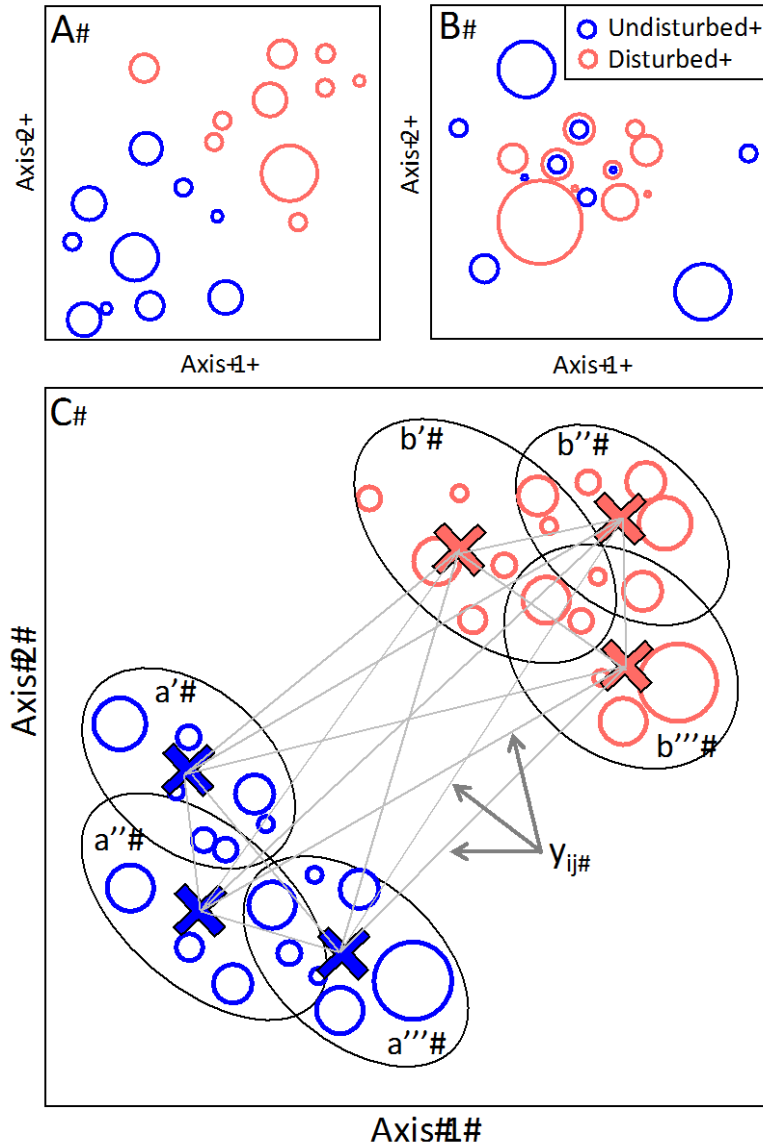
Figure 3.1 Multidimensional trait space. Each point represents a combination of functional trait states ("trait combination"), and point size reflects the abundance of individuals with that trait combination. Blue points represent trait combinations in an undisturbed community and red points in a disturbed community (as per Mouillot et al. 2013b). (A) Two communities with non-overlapping trait composition (e.g., complete functional turnover between communities). Disturbance causes a shift in the location of each community's central tendency, or *functional centroid*. (B) Species in the disturbed community occupy a smaller area of trait space than the undisturbed community and thus contain a narrower *range* of trait combinations (e.g., functional convergence). (C) Multiple communities of each disturbance type to demonstrate the nested levels of biological information that can be represented in trait space. Ellipses a', a'' and a''' surround the trait combinations of species in three replicate samples of undisturbed communities, and ellipses b', b'' and b''' encircle three replicate samples of disturbed communities. The Xs indicate the location of the multivariate functional centroids of each community, and the grey lines represent the distances between functional centroids (y_{ij}s). If all species points were removed and only the functional centroids remained, panel C would become an ordination of six communities in trait space. Individual-scale information could also be included in this representation, nested within each point.

While it is relatively easy to create plots of multivariate trait space, we still lack a framework for consistently using these techniques to select quantitative approaches that address ecological questions. We believe that visualizations of ecological phenomena in multivariate trait space can fill this gap. Our approach is straightforward, intuitive, and quantitative: (1) design research questions based on ecological theory and system-specific ecology; (2) evaluate graphical hypotheses of expected differences in trait space; (3) select a subset of traits to address the research questions; (4) select or develop metrics that quantify the characteristics of trait space necessary to test the hypotheses; and (5) challenge the hypotheses with data and interpret differences in trait space in light of the results (Figure 3.2). Steps 1, 3, and 5 are reasonably well established, and we illustrate their execution in a case study. Our primary contribution is to facilitate the selection and development of appropriate FD metrics for hypothesis testing (step 4) by visualizing ecological hypotheses in trait space (step 2). This process can indicate which combinations of metrics are required to detect relevant changes in trait space. The selection of appropriate metrics for hypothesis testing has been a conceptual hurdle in the current literature; explicitly linking ecological hypotheses to functional metrics will help researchers rigorously address a broad array of ecological questions.

Step 1. Research questions are designed using system-specific ecological knowledge and ecological theory. How will a trait-based approach address outstanding questions regarding ecological processes?

Step 2. The arrangement of trait combinations in multidimensional trait space (Fig. 1) is used to visualize and evaluate hypotheses regarding changes in functional composition of communities. We provide five hypotheses of community assembly in response to disturbance (Fig. 3), although this approach can be applied to other ecological contexts as well. Hypotheses are described in the main text.

Step 3. Outcomes of FD analyses are highly sensitive to trait selection (Petchey and Gaston 2006), and the characteristics of the traits will determine which FD metrics are mathematically feasible and biologically informative (Podani 2009, McCune 2014).

Step 4. An extensive literature guides researchers to select metrics or combinations of metrics to address each hypothesis given the trait subset (Table 1). New metrics may be required to capture relevant changes in trait space, as we highlight with the development functional distance to quantify functional turnover.

Step 5. This step follows the scientific method and is outlined with the case study. Theory and system knowledge play a key role in interpreting outcomes of tests using FD metrics.

Figure 3.2 A graphical hypothesis-evaluation framework. We use graphical hypotheses representing ecological patterns to inform the selection of quantitative functional diversity metrics and guide the interpretation of results in the context of system-specific ecology.

Graphical hypotheses. We use visualizations of ecological hypotheses in trait space to motivate informed metric selection (or development) and quantitative hypothesis testing (Fig. 3). Our visualization of *hypotheses* complements the visualization of *metrics* in Mouillot et al. (2013b); however, in our approach trait space also forms the basis for linking questions to quantitative methods, not just as a way to conceptualize the metrics themselves. These ecological hypotheses are not mutually exclusive, as we illustrate in the context of disturbance. We consider the role of disturbance as a categorical environmental driver (disturbed/undisturbed) to highlight the complementary nature of our work and that of previous authors (Mouillot et al. 2013b). However, the approach can be readily extended to general questions of spatial or temporal differences in community structure, beyond the binary treatments described below. Further, it is not limited to tests of disturbance ecology; our intent is to provide a visualization tool to guide hypothesis testing and the selection of analytical methods that may be useful across a variety of systems and ecological questions.

We present five graphical hypotheses of how disturbed and undisturbed communities may differ in multivariate trait composition (Figure 3.3). We use the term "graphical hypotheses" to refer to visual representations of ecological phenomena in multivariate trait space, not a probabilistic graphical modeling approach (Koller et al. 2007). The hypotheses represent fundamental ecological phenomena that are commonly observed in published studies. They can be modified and applied broadly to describe patterns of community distinction in many systems. The hypotheses draw from the fields of community assembly theory (Samuels and Drake 1997, Leibold et al. 2004, Leibold and McPeek 2006), restoration ecology (Matthews and Spyreas 2010, Ruhí et al. 2013, Laughlin 2014), disturbance ecology (Houseman et al. 2008, Mouillot et al. 2013b), and functional ecology (Mouchet et al. 2010, Mason and de Bello 2013, Mason et al. 2013, Mouillot et al. 2013b), among others. Our goal is not to pioneer novel hypotheses of community assembly but instead to demonstrate how to use FD analyses to test this broad set of hypotheses in a rigorous and ecologically informed manner.

We illustrate our graphical hypotheses with two example communities, representing disturbed and undisturbed conditions (Figure 3.3). We represent differences in functional trait composition between the communities in a multidimensional trait space as described above. In most applications of trait space in the published literature, each unique trait combination represents a species and concentric points represent functionally redundant species that share trait combinations (Rosenfeld 2002). However, it is also possible that species' trait combinations could vary within species via genetic variation, phenotypic plasticity, or other processes (Miner et al. 2005, Bolnick et al. 2011). Therefore, we refer to points in trait space as "trait combinations." The hypotheses were designed to incorporate species abundances but may be subset and modified for datasets containing only presence/absence information. While each hypothesis in Figure 3.3 represents one disturbed community sample and one undisturbed community sample, the basic framework and quantitative analyses are intended to be performed

on replicate communities, such as replicates within treatments, sites, or time points, as we demonstrate with the case study.
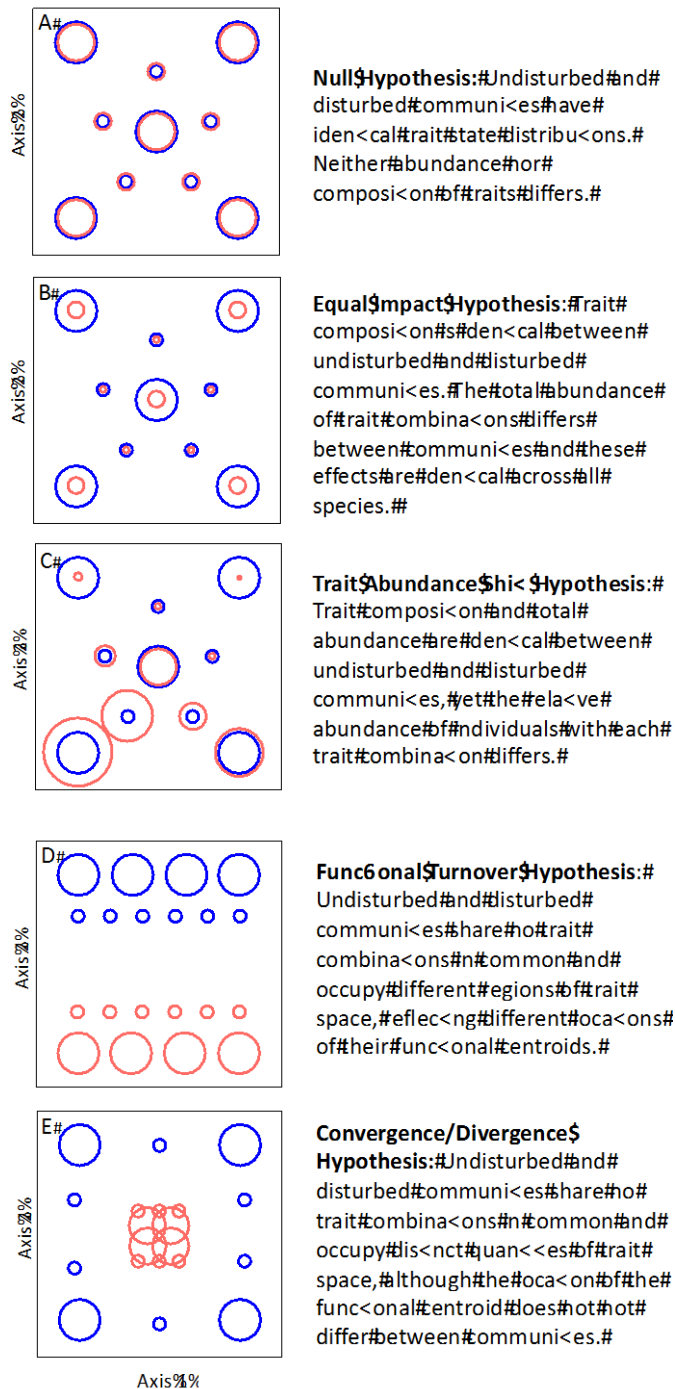
Figure 3.3 Five graphical hypotheses of how disturbance may alter the distribution of trait combinations in multidimensional trait space (hereafter "trait space"). Each hypothesis is a multivariate ordination, where each point represents a trait combination and circle size is determined by the abundance of individuals with that particular combination. Blue circles represent trait combinations of species in an undisturbed community, and red circles represent those of a disturbed community (as per Mouillot et al.

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2013b). For illustration, each community contains ten trait combinations (or species), and we assume that both communities exist within the same regional species and trait pools.

We present the following hypotheses:

H1: Null Hypothesis. In this scenario, there is no difference in trait composition or the total abundance of individuals with different trait combinations between disturbed and undisturbed communities. In other words, there are no differences in the abundance, range, or central tendency of trait states. The two communities may be exposed to similar community/trait structuring processes (Weiher and Keddy 1995) or may contain distinct species with the same trait combinations, reflecting complete functional overlap (Mouillot et al. 2013a). Note that insufficient evidence to reject the null hypothesis may occur because the selected traits are inadequate to detect a real difference between communities, emphasizing the importance of careful selection of ecologically relevant traits (Step 3).

H2: Equal Impact Hypothesis. The range and central tendency of trait combinations do not differ between disturbed and undisturbed communities, yet the total abundance of individuals differs and these impacts are equal across all trait combinations. Equal impacts might arise from largely abiotic processes that have similar per-capita effects across species. For example, this could occur if a disturbed community contains a smaller quantity of a shared resource or has poorer overall habitat quality than an undisturbed community, resulting in overall lower species abundances. Alternately, mild nutrient enrichment may generate the same pattern but opposite in effect, in which all trait combinations increase in abundance by the same amount following disturbance.

H3: Trait Abundance Shift Hypothesis. All trait combinations present in the undisturbed community are also present in the disturbed community and vice versa; however, the number of individuals with particular trait combinations differs between communities. In other words, traits that are favorable in one community may be unfavorable in the other, producing differences in the distribution of abundances in trait space but no differences in the range identity, or overall number of trait combinations. This pattern could occur if conditions under each disturbance type are not extreme enough to cause the local extirpation of species (taxonomic extinction) or trait combinations (functional extinction) as in the Functional Turnover or Convergence/Divergence Hypotheses, below. Changes in the abundance of some trait combinations relative to others, without the complete loss or addition of any one combination, may be important warning signs of impending functional extinctions and functional turnover (Säterberg et al. 2013).
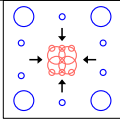
H4: Functional Turnover Hypothesis. If disturbance introduces or eliminates some trait combinations altogether, disturbed and undisturbed communities may share few species or trait combinations in common and occupy distinct regions of trait space. In this case, the location of the central tendency of each community differs, while the range and total abundance of trait combinations may remain unchanged. This outcome could occur if disturbed and undisturbed

communities are exposed to different environmental conditions that reduce the persistence of species with particular trait combinations from the shared regional species pool, representing species sorting and environmental turnover of species/traits (Poff 1997, Leibold et al. 2004, Webb et al. 2010). Functional turnover may also be expected in classic Clementsian succession in which species at a single site are replaced through time (Clements 1916), which could result in a change in a community's central tendency in trait space. In the next section ("Selecting metrics to test the hypotheses"), we develop and describe a new metric for detecting functional turnover that can be applied to test this hypothesis.

H5: Convergence/Divergence Hypothesis. Of all of the hypotheses, convergence/divergence is the most established in the current FD literature, likely because of its intuitive interpretation in the context of ecological theory. Graphically, convergence occurs when species in the disturbed community occupy a smaller area of trait space than those in the undisturbed community (Mason et al. 2005), reflecting a smaller range of trait values. This could occur if disturbance acts as an environmental filter (Poff 1997, Leibold et al. 2004, Grime 2006) that reduces the trait combinations in the disturbed community to a subset of those existing in the undisturbed community (Leibold et al. 2004, Webb et al. 2010) or if functionally homogenous species replace a more functionally diverse community. Alternately, disturbance may create functional niches for colonization of the disturbed community by species that were excluded from the undisturbed community, causing functional divergence (e.g. Cadotte 2007). Divergence can be represented as an expansion of the area species occupy in trait space. Expansion may occur if disturbance causes the local extinction of a competitively dominant species or keystone predator (Paine 1966), or facilitates the establishment of invasive species without supplanting native taxa (e.g., Hejda and de Bello 2013).

Selecting metrics to test the hypotheses. A key challenge we seek to address is the selection of quantitative methods that capture the changes in trait space necessary to demonstrate support for one or more of the hypotheses. Table 3.1 illustrates our decision process to select quantitative metrics prior to analyses that test the five graphical hypotheses (Step 4). First, we used the graphical representations to determine which aspects of the functional space must be measured to test the hypotheses of ecological change. Then we identified metrics or combinations of metrics with mathematical properties that quantify these aspects and can be used to compare them between disturbed and undisturbed communities. Our recommendations come from consulting the extensive quantitative FD literature (Petchey et al. 2004, Mason et al. 2005, Petchey and Gaston 2006, Mouchet et al. 2010, Cadotte et al. 2011, Schleuter et al. 2011, Kleyer et al. 2012, de Bello et al. 2013, Mason et al. 2013, Mouillot et al. 2013b, Spasojevic et al. 2014). We did not identify an intuitive existing approach we believed was suitable to test differences in the location of the central tendency as in the Functional Turnover Hypothesis, so we designed a new metric, *functional distance* (described below). The final step of metric and method selection is to determine appropriate statistical hypothesis tests.

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Table 3.1. Using graphical hypotheses to select quantitative metrics. This table represents our decision process to select metrics for testing hypotheses about responses to disturbance. "Metric requirements" are factors considered when selecting each metric, as described in the text. "Hypothesis test" indicates which tests are needed to support each hypothesis. Hypotheses are not mutually exclusive and support may be found for multiple hypotheses at once. Note: The graphical hypotheses depicted in Fig. 3 are simplified diagrams that compare a single disturbed community replicate with a single undisturbed community replicate, but hypothesis-testing requires that there are multiple replicates of communities in Treatments A and B (undisturbed and disturbed).

Hypothesis	Metric requirements		Metric	Hypothesis test
Null	-		All	None of the following metrics differ between treatments.
Equal Impact	Detect differences in abundance between communities that are evenly distributed across trait combinations.		Total abundance (TAb)	Total abundance of trait combinations differs between A and B (Welch's t-test). FDisp, FDist, and FRic do not differ.
Trait Abundance Shift	Detect differences in the relative abundance of traits in each community		Functional dispersion (FDisp, Laliberté & Legendre 2010)	Functional dispersion differs between A and B (Welch's t-test). FDist and FRic do not differ. TAb may or may not differ.
Functional Turnover	Detect differences in the location of communities' functional centroids in trait space		Functional distance (FDist, this manuscript)	Functional distance between A and B is greater than null expectation (Mixed effects modeling). FDisp will also differ. FRic and TAb may or may not differ.
Convergence/Divergence	Detect differences in the range of trait space occupied by each community		Functional richness (FRic, Villéger et al. 2008)	Functional richness differs between A and B (Welch's t-test). FDisp will also differ. FDist and TAb may or may not differ.

We identified two published FD metrics that are appropriate to test the graphical hypotheses: functional richness (Villéger et al. 2008) and functional dispersion (Laliberté and Legendre 2010), and created a third, called functional distance. When used in combination with the abundance of species or trait combinations, these metrics enable quantitative tests of how functional trait differences between disturbed and undisturbed communities support or do not support the five hypotheses. The three multivariate metrics are derived from pairwise Gower dissimilarity (Gower 1971) in trait composition between replicate communities. Next we describe how and why our evaluation of the graphical hypotheses led us to select each of the FD metrics. We also discuss metric limitations and cases where combinations of metrics may be required.

Functional dispersion. The Trait Abundance Shift Hypothesis involves differences in the proportion of individuals with particular trait combinations that do not result in the addition or

loss of any combinations entirely, as occurs with the Functional Turnover and Convergence/Divergence Hypotheses. To demonstrate differences in the proportional abundance of trait combinations that would indicate a trait abundance shift, one must quantify the distribution of abundances in trait space. Functional dispersion measures the mean distance of all species to the abundance-weighted central tendency of a community (Laliberté and Legendre 2010), where the functional centroid is a composite mean trait value for all species in a community that is weighted by species abundances. Conceptually, functional dispersion quantifies the mean difference between species by comparing each species in the community to a hypothetical representative species (the centroid). Differences in dispersion between disturbed and undisturbed communities suggest that disturbance favors some trait combinations over others, and this can be reflected in differences in the relative abundance of species with different trait combinations.

Functional richness. Determining support for the Convergence/Divergence Hypothesis requires a metric that is not dependent upon the relative abundance of trait combinations. Functional richness measures the overall area of trait space (convex hull) occupied by species in a community, irrespective of abundance (Mason et al. 2005, Cornwell et al. 2006, Villéger et al. 2008, Podani 2009). Significant differences in this metric between disturbed and undisturbed samples indicate disturbance-induced convergence or divergence in functional composition that may not be associated with a shift in the location of the functional centroid (Villéger et al. 2008). This metric is the one most commonly used in existing FD studies that test hypotheses about responses to disturbance (e.g., Mason et al. 2012, Laliberté et al. 2013), likely because differences in this metric are the most straightforward to interpret in the context of a system's ecology.

Functional distance: a novel metric. Functional dispersion detects changes in the relative abundance of trait combinations and is important to support or refute the Equal Impact, Trait Abundance Shift, and Convergence/Divergence Hypotheses. However, to test whether disturbance causes the addition or loss of trait combinations in an entire region of trait space as in the Functional Turnover Hypothesis it is also necessary to determine whether disturbance affects the location of a community's central tendency, irrespective of species abundances. The distance between the functional centroids of two communities (y_{ij}) measures differences in trait space that may result from low functional overlap between the communities. While many metrics exist, we did not find an intuitive, published metric that could account for the non-independence of pairwise comparisons between replicate communities, so we created a novel metric that we refer to as *functional distance*. We define functional distance as the distance between the non-abundance-weighted functional centroids of two communities in trait space (grey lines in Table 3.1C). While it is straightforward analytically to calculate the functional distance between two communities in multidimensional space, calculating pairwise distances between multiple communities that have been grouped (by sampling occasion, site, or treatment), as in the case of replicate disturbed and undisturbed communities, is more complex. Multiple pairwise distances

associated with a given site or community (values within a row or column in a community matrix) are non-independent, and this non-independence creates a correlated error structure that biases calculation of meaningful confidence intervals or standard errors (Clarke et al. 2002). We address this problem using mixed effects models with disturbed/undisturbed as a fixed effect and community as a random effect. A similar method has been applied with genetic distances (Van Strien et al. 2012) and landscape distances (Bellamy et al. 2003), but to our knowledge this is its first application to measure functional distance.

To quantify functional distance, we converted the community matrix to a presence/absence matrix of 1s and 0s and then calculated the functional centroid for each community from the Gower distance matrix. This is easily obtained using function fdisp() in the R package FD (Laliberté and Legendre 2010, Laliberté and Shipley 2011). This function applies principal coordinates analysis to the distance matrix to generate centroid coordinates for each community and corrects for negative eigenvalues as described by Anderson (2006). Then, we calculated pairwise Euclidean distances between the centroids of all disturbed and undisturbed communities (functional distances) and examined the effect of disturbance on these distances using a mixed-effects model of the following form:

$$Y_{ij} = \mu + \alpha_i + \beta_j + \varepsilon_{ij}$$

Where Y_{ij} is the functional distance between the centroids of communities i and j, μ is the fixed effect of disturbed/undisturbed (0/1), α_i and β_j are random effects to account for correlations between pairwise distances that have a community in common, and ε_{ij} is an independent error term. Following the suggestion of Van Strien et al. (2012), who addressed this issue with genetic distances, we used Markov chain Monte Carlo simulation to repeatedly resample distances from the distance matrix and compare models with and without the disturbance term. Finally, we determined model performance by examining posterior means and the 95% credible interval. When the superior model includes the disturbance term and the credible interval for the disturbance term does not overlap zero, communities i and j have demonstrated a disturbance-induced shift in multivariate trait space.

3.4   Combinations of metrics

In most cases, a combination of metrics is necessary to determine support for the hypotheses . For example, support for the Equal Impact Hypothesis requires evidence of a difference in total abundance and the lack of a difference in functional dispersion, functional richness, and functional distance. The Trait Abundance Shift Hypothesis, Functional Turnover Hypothesis, and Convergence/Divergence Hypothesis all generate differences in functional dispersion. Therefore, determining which hypothesis or hypotheses are supported in a particular case study also requires the inclusion of functional distance and functional richness. For example, disturbance may cause the relative abundance of trait combinations to shift without functional turnover or convergence/divergence, but convergence/divergence and functional turnover always

accompany shifts in trait abundances. These nuances are ecologically informative and understanding them is essential to making appropriate inferences from FD studies.

Under very rare circumstances further scrutiny may be necessary to differentiate among hypotheses. For example, if disturbance causes species to be replaced by other taxa with trait combinations that are the same distance from the functional centroid, this functional turnover would not be detected by any of metrics combinations we propose. Unlikely situations like this one highlight the importance of visualizing and interpreting differences in trait space in light of system-specific ecological knowledge. Such cases can usually be avoided by incorporating ecological observations, or by combining taxonomic and functional analyses, as we demonstrate with our case study. Integrating species and trait information will produce a fuller understanding of how communities function and allow researchers to isolate and interpret any irregularities.

3.5   A case study

We demonstrate the framework with a published dataset on stream invertebrate communities before and after catastrophic stream drying (Bogan and Lytle 2011). In this study, researchers sampled the aquatic invertebrate community in a small, isolated stream (French Joe Canyon) in southeast Arizona for eight-years (2002-2009), before and after a severe drought and resultant stream drying event. Samples taken before drought were classified as "undisturbed" and those taken after as "disturbed."

Step 1: Generate research question.

We asked: how does stream drying affect the functional composition of aquatic invertebrate communities?

Step 2: Evaluate graphical hypotheses.

The five hypotheses are all ecologically feasible in this case study, and we imagine this will be true in many other applications as well. Taxonomic analyses documented species turnover when drought-sensitive taxa were eliminated from aquatic communities and replaced by taxa that were resilient to drought (Bogan and Lytle 2011). Consequently we expected this case study to support the Functional Turnover Hypothesis. However, given the limited information on how aquatic communities respond to unprecedented drought and the potential for multiple hypotheses to be at play concurrently, we set out to test all five hypotheses.

Step 3: Select the trait subset.

Outcomes of FD analyses are highly sensitive to trait identity, and the inclusion of more traits does not necessarily result in more accurate or informative outcomes (Petchey and Gaston 2006). We used background knowledge of aquatic invertebrate communities to choose seven categorical traits for this analysis that are associated with biological responses to drought in arid-land

streams: body size, functional feeding group, dispersal ability, locomotion, voltinism, respiration, and diapause (Boersma et al. 2014, Schriever et al. 2015).

Step 4: Select the quantitative metrics.

We used the metric combinations and statistical tests described in Table 1 to evaluate the five hypotheses. Because of our expectation of functional turnover, it was important to include the novel metric, *functional distance*, since neither functional richness nor functional dispersion alone could test the Functional Turnover Hypothesis. After calculating the metrics and examining their empirical distributions, we compared total abundance, richness and dispersion between disturbed and undisturbed groups using Welch's t-tests. We calculated functional distance using the mixed effects modeling approach described earlier. All analyses were conducted using R version 2.14.1 (R Development Core Team 2011) and packages MCMCglmm, lme4, FD, and vegan (Hadfield 2010, Bates et al. 2011, Laliberté and Shipley 2011, Oksanen et al. 2012).

Step 5: Challenge hypotheses with data and interpret results in light of system-specific ecology.

Counter to our expectations, we did not detect a difference in the location of the functional centroid, i.e., in the *functional distance* between disturbed and undisturbed communities (MCMC, lower credible interval = -0.001901, upper credible interval = 0.019696). This indicates a lack of support for the Functional Turnover Hypothesis. Total abundance differed between disturbed and undisturbed communities (Welch's t-test, t = -3.3107, d.f. = 16.133, p = 0.004378), indicating a lack of support for the Equal Impact Hypothesis. Despite the lack of functional turnover, there was evidence that functional richness was lower in the disturbed post-drying communities than in the undisturbed pre-drying communities (Welch's t-test, t = 2.541, d.f. = 14.447, p = 0.023) and there was moderate evidence that functional dispersion exhibited the same pattern (Welch's t-test, t = 1.920, d.f. = 17.959, p = 0.071). The reduction in functional richness following stream drying indicates trait convergence and supports the Convergence/Divergence Hypothesis.

System-specific ecology is as important when interpreting the results of FD analyses as it is when generating research questions. Disturbed post-drought communities experienced an influx of colonists when flow returned after the stream drying event (Bogan and Lytle 2011), and these new colonists were functionally similar to some (but not all) of the species present in the community before drying. The functionally homogeneous colonists replaced taxa that had diverse trait combinations at the edges of multivariate trait space, which produced the overall reduction in functional richness we observed, without a difference in functional turnover.

3.6 Summary

Our hypothesis-evaluation framework was motivated by the need for an intuitive and ecologically informed way to select quantitative FD methods prior to data analysis. The growing number of quantitative FD approaches makes it essential that researchers justify metric selection

in light of trait-based hypotheses, rather than simply adopting published techniques without assessment. Our framework facilitates this process by using graphical hypotheses in multivariate trait space to guide the selection, application, and interpretation of quantitative methods. We propose a set of metrics to test common ecological hypotheses of functional community assembly, including a new metric to measure functional distance among communities. This approach will encourage more consistent application of multivariate FD methods in a rigorous manner, while honoring the importance of system-specific ecological knowledge and observed community assembly patterns.

Our five graphical hypotheses represent functional trait responses to environmental drivers in two categories (in our example: disturbed and undisturbed), but we envision many applications for which two categories are sufficient (e.g., treatment/control, before/after). Moreover, our flexible approach could easily be adapted to accommodate more than two groups, such as multiple time points or samples along a gradient or to consider effect traits and test hypotheses concerning ecosystem functioning (Naeem and Wright 2003, Suding et al. 2008). The *a priori* selection of quantitative tools to address hypotheses also helps researchers identify potential needs to design novel metrics if appropriate ones do not exist, as we have done here with our functional distance metric to measure functional turnover among replicate communities.

The recent surge in FD studies suggests that a functional approach to ecology is an appealing means to detect community assembly patterns that transcend specific ecosystems. However, it is challenging to conceptualize ecological patterns in multivariate trait space and select quantitative methods to discern among them. Our framework will address this challenge and thereby increase the applicability of functional approaches and enable functional ecology to continue to grow into a practical and rigorous discipline.

3.7   Acknowledgements

4 Using niche-based occupancy models to estimate probability of species occurrence.

Synopsis: This chapter uses a Bayesian occupancy model approach to understand which organismal traits might be important for determining biodiversity patterns on the landscape. The approach also incorporates the detectability of species -- the notion that a species might be present at a site but not collected in a sample.

4.1 Introduction

Confirming the occurrence of a species is a two-fold process. First, the species must be present at the time sampling occurs (ecological process) and second, given that the species is present, the surveyors must be able to detect the presence of the species (detection process). Accurate quantification of species richness at any point in time and space requires robust characterization of ecological and detection processes. This hierarchical framework lends itself to a Bayesian occupancy modeling approach, which not only estimates biodiversity at a given site, but also estimates the detection rate of species (MacKenzie *et al.* 2008).

We used detection data for 110 macroinvertebrate taxa in Ramsey, Garden, Huachuca and Woodcutters canyons in the eastern Huachuca Mountains, Arizona. These taxa were selected to represent the full taxonomic and functional (trait) diversity of macroinvertebrate communities in the Huachuca Mountains. According to data collected from our array of electrical resistance sensors (Jaeger and Olden 2012) the stream locations were classified as perennial or non-perennial (intermittent or ephemeral). Sampling sites also varied in their microhabitat, with some representing riffles and others representing pools. Because the occupancy models require replicate sampling to estimate species detection rates, we grouped the sampling sites into the following regions: Garden (sites: GaC, GaS, GaW), Huachuca (sites: HuC, HuG, HuL, HuM), Ramsey (sites: RaU1, RaU2, RaU3), and Woodcutter (sites: WoU1, WoU2, WoU3). We assumed that sites within a region were homogenous – a species present in one site of a region would also be present at all sites of that region. Thus, temporal replication within a season was substituted with spatial replication. Species exhibited a range of life-history traits with varying maximum body sizes, number of generations per year, dispersal mode, and ability for diapause.

Our model assumed that occupancy (presence/absence), $z(i, j, t)$, for species $i = 1 \dots N$ in region $j = 1 \dots J$ was fixed within a sampling season $t = 1 \dots T$, but could change between seasons. For each sampling season, occupancy was the outcome of a Bernoulli trial, $z(i, j, t) \sim \text{Bern}(\psi_{ij}(t))$ where $\psi_{ij}(t)$ is the probability that species i is present in region (canyon) j at sampling season t, and $z(i, j, t) = 1$ if the species is present and zero otherwise. In the first sampling season, occupancy probability $\psi_{ij}(1)$ is estimated from a combination of the first season of sampling data and the estimated detection probabilities (see section on the Detection Process). For every other season, occupancy probability depended on the occupancy state of the previous season and

the species- and region-specific persistence and colonization ability. If a species was present in the preceding season, then the probability that it is also present in the current season depends on the species' persistence probability. If a species was absent in the preceding season, then the probability that it is present in the current season depends on the species' colonization probability. Figure 4.1 summarizes these transitions. So, for seasons $t = 2 \ldots T$, we calculated occupancy probability as:

$$\psi_{ij}(t) = z(i,j,t-1) \cdot \phi_{ij} + [1 - z(i,j,t-1)] \cdot \gamma_{ij},$$

where ϕ_{ij} and γ_{ij} are the persistence and colonization probabilities of species i at region j in season t-1, respectively.
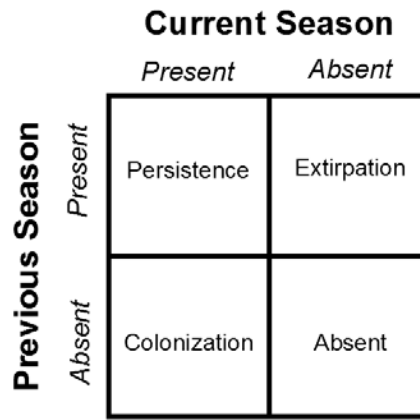
Figure 4.1. Possible transitions of species occupancy between sampling seasons.

In summary, our model estimated the following ecological characteristics for each species i at every region j: initial occupancy probability $\psi_{ij}(1)$, persistence probability ϕ_{ij}, and colonization probability γ_{ij}. See Figure 4.2 for a schematic of the ecological process.
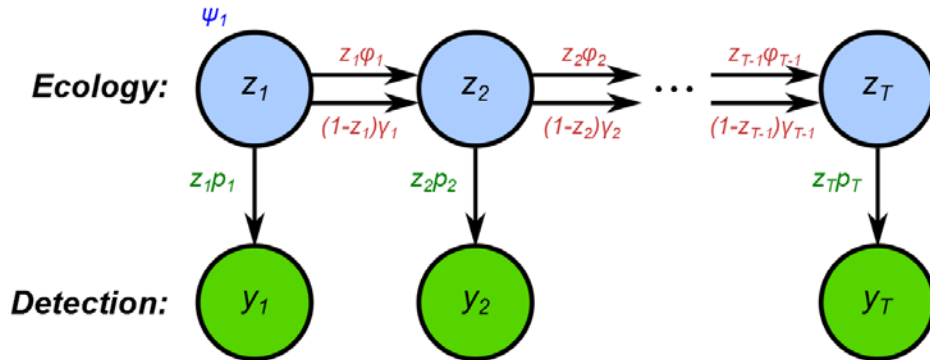
Figure 4.2 Schematic of hierarchical modeling framework. Blue circles represent occurrence states while green circles represent detection states. In the first sampling season, a species is present ($z_1 = 1$) with probability ψ_1. Given that it's present, surveyors can detect it ($y_1 = 1$) with probability p_1. For all following seasons t, occupancy probability is given by $\psi_t = z_{t-1}\phi_{t-1} + (1 - z_{t-1})\gamma_{t-1}$.

In addition, we posited that ecological and detection rates could co-vary with both stream attributes and species life-history traits. We also posited that persistence, colonization, and detection rates may vary among seasons or years. The covariates were chosen based on environmental attributes and species traits provided by field data, as well as what we believed to be plausible interactions between covariates (Table 4.1). Because the rates are represented as probabilities that can range from 0 to 1, we incorporated the contribution of covariates to these rates using logistic regression. Logistic regression uses the logit function to transform probabilities into a range of negative infinity to infinity, and allows for a linear fit with model parameters. To get the probabilities back, we use the inverse-logit function (e.g. logit(0.5) = 0).

Table 4.1 Descriptions of categorical covariates used in logistic regression models.

Name	Description
Region	
Perennial	Streams that flow continuously year-round, as opposed to ones that dry up during certain times of year
Riffle	Sampling sites that consist predominantly of riffle microhabitat, as opposed to pools
Species	
Size2	Species of moderate size
Size3	Species of large size
Volt2	Species that have 1 generation per year
Volt3	Species that have >1 generation per year
Disp2	Active aquatic dispersers
Disp3	Passive aerial dispersers
Disp4	Active aerial dispersers
Diap2	Species whose diapause ability is indeterminate
Diap3	Species confirmed to not diapause
Time	
Spring	Spring sampling seasons
Monsoon	Monsoon sampling seasons
WY2011	Sampling seasons occurring from Fall 2010 to Monsoon 2011 (Water Year 2011)
WY2012	Sampling seasons occurring from Fall 2011 to Monsoon 2012 (Water Year 2012)
Interactions	
Perennial:Disp2	Active aquatic dispersers occuring in perennial sites
Perennial:Disp3	Passive aerial dispersers occuring in perennial sites
Perennial:Disp4	Active aerial dispersers occuring in perennial sites
Perennial:Diap2	Indeterminate diapause species occuring in perennial sites
Perennial:Diap3	Non-diapause species occuring in perennial sites
Perennial:Spring	Sampling occurring in spring at perennial sites
Perennial:Monsoon	Sampling occurring in monsoon season at perennial sites
Perennial:WY2011	Sampling occurring during Water Year 2011 at perennial sites
Perennial:WY2012	Sampling occurring during Water Year 2012 at perennial sites

4.2 Model selection

With 2 regional environmental variables, 4 trait covariates, 2 temporal covariates, and 4 interaction considerations for each ecological or detection process, there were a total of 2^{44} different regression models to explore – ignoring temporal covariates for initial occupancy rates and not accounting for the fact that interactions force other covariates to be included. Given the

large number of covariates, we expected that the full model with all covariates would be overparameterized (e.g. due to correlations among trait covariates). Thus, we used a Bayesian approach for model simplification (Burton *et al.* 2012). In a separate model, we included a latent binary variable, w_c, for every covariate c that represented whether or not the corresponding covariate should be included in the model. An inclusion parameter of $w_c = 1$ suggests that the corresponding covariate is included in the "best" model (Burton *et al.* 2012), and more support is given when $w_c = 1$ occurs with higher frequency. Thus, we selected the median model (Barbieri and Berger 2004), where the covariate structure includes only the covariates where $w_c = 1$ in more than half of the samples.

4.3   Model implementation

We implemented all models in program JAGS version 3.4.0 (Plummer 2003) via the package R2jags to interface with program R (Su and Yajima 2012). Inference of inclusion probabilities and full model parameters was based off of 20,000 samples from a single chain of Markov Chain Monte Carlo (MCMC) iterations after a burn-in of 5,000. Inference of model parameters for simplified models was made from 2,000 samples of the posterior distribution obtained from a single chain of 20,000 Markov Chain Monte Carlo (MCMC) iterations after a burn-in of 5,000 and with a thin rate of 10. We used vague, normal priors for all the parameters and random initial values. We also used priors of 0.5 for the probability that a covariate was included in the model, so that each covariate was just as likely to be included as not. The MCMC procedure was visually validated for convergence using multiple chains and the Gelman-Rubin statistic (Gelman *et al.* 2004).

4.4   Model results

Parameter estimates from the full model – where all covariates were incorporated into each process – were variable (Table 4.2 -Table 4.5). Model selection showed strong support for microhabitat and diapause ability as strong covariates for initial occupancy rate (Table 4.2). For taxa persistence, regional hydrology, year, and voltinism were strong covariates, and there was also support for an interaction between hydrology and study year. Hydrology, dispersal mode, diapause ability, and season were supported covariates of colonization rate, and there was also evidence for an interaction between hydrology and season (Table 4.4). Finally, only diapause ability and sampling year had strong support as covariates for detection rate (Table 4.5).

We constructed a Bayesian hierarchical model based on the covariates selected in the median model (Table 4.6). Generally, species richness was high during the first sampling season. Initial occupancy rate was significantly lower in riffle microhabitat than in pool microhabitat. In addition, taxa with indeterminate diapause ability were significantly more present in the first sampling season than other taxa.

On average, persistence between seasons was lower than 50%. However, persistence of taxa between seasons was significantly higher in perennial streams than in non-perennial streams. Persistence was also significantly greater in Water Year 2011 than in the rest of the study period.

Combined, persistence was estimated to be practically guaranteed for taxa residing in perennial streams. Though not statistically significant, persistence was lower for taxa with one generation per year compared to other taxa.

Colonization rates were significantly lower in perennial streams, and higher during the monsoon seasons. Colonization also tended to be lower during the spring seasons, for active dispersers, and for taxa that do not diapause. Generally, detection of taxa was poor, particularly for taxa that did not exhibit diapause. However, detection rates increased significantly throughout the study period (between years).

Macroinvertebrate biodiversity was generally lower in riffles than in pools for perennial streams, while biodiversity was similar between paired pool and riffle sites of non-perennial streams (Figure 4.3). Biodiversity did not fluctuate drastically in perennial streams, owing to high persistence rates and low colonization rates. On the other hand, biodiversity in non-perennial streams was lower in the spring and monsoon seasons than in the fall.

Table 4.2 Posterior summaries of initial occupancy covariate parameters in the full model (without inclusion parameters) and inclusion probabilities of each parameter.

Parameter	Mean	SD	95% CI	Inclusion Probability[†]
Intercept	3.6	1.4	(0.89, 6.22)	-
Riffle Microhabitat	-1	0.3	(-1.66, -0.31)	0.93[**]
Indeterminate Diapause	-0.7	1.5	(-3.35, 2.41)	0.82[**]
No Diapause	-0.3	1	(-2.37, 1.71)	
Perennial Stream	0.6	1.1	(-1.74, 2.77)	0.37
1 Generation/Year	0.3	0.5	(-0.68, 1.25)	0.36
>1 Generation/Year	-0.8	0.5	(-1.77, 0.26)	
Active Aquatic Disperser (AAqD)	0.8	1.4	(-1.93, 3.53)	
Passive Aerial Disperser (PAeD)	0	1.6	(-3.04, 3.1)	0.36
Active Aerial Disperser (AAeD)	-0.6	1.2	(-2.87, 1.59)	
Moderate Size	-0.1	0.4	(-1, 0.72)	0.17
Large Size	-1.1	0.5	(-1.93, -0.11)	
Perennial:Indeterminate Diapause	1.5	1.4	(-1.38, 4.1)	0.13
Perennial:No Diapause	-0.2	1.1	(-2.3, 1.87)	
Perennial:AAqD	0.9	1.4	(-1.97, 3.62)	
Perennial:PAeD	0	1.6	(-2.99, 3.07)	0.06
Perennial:AAeD	-0.6	1.1	(-2.89, 1.57)	

† [**] denotes covariates with strong support (p > 0.7); [*] denotes covariates with some support (p > 0.4)

Table 4.3 Posterior summaries of persistence covariate parameters in the full model (without inclusion parameters) and inclusion probabilities of each parameter.

Parameter	Mean	SD	95% CI	Inclusion Probability[†]
Intercept	3.4	1.4	(1.02, 6.5)	-
Perennial Stream	-0.2	1.2	(-2.61, 2.04)	1.00[**]
WY2011	1.7	1.1	(-0.48, 3.89)	1.00[**]
WY2012	0	1.6	(-2.98, 2.96)	
Perennial:WY2011	1.3	1.2	(-0.95, 3.76)	0.77[**]
Perennial:WY2012	0	1.6	(-3.28, 3.05)	
1 Generation/Year	-0.5	0.7	(-2.01, 0.79)	0.57[*]
>1 Generation/Year	1	1	(-0.81, 3.18)	
Active Aquatic Disperser (AAqD)	0.6	1.3	(-1.92, 3.27)	0.45[*]
Passive Aerial Disperser (PAeD)	0.1	1.6	(-3.02, 3.17)	
Active Aerial Disperser (AAeD)	0.5	1.1	(-1.58, 2.88)	
Spring Season	0.9	1.4	(-1.81, 3.74)	0.44[*]
Monsoon Season	-0.6	1.2	(-2.98, 1.81)	
Perennial:AAqD	0.8	1.3	(-1.71, 3.37)	0.36
Perennial:PAeD	0	1.6	(-3.07, 3.17)	
Perennial:AAeD	-0.1	1.2	(-2.44, 2.05)	
Perennial:Spring	0.8	1.3	(-1.56, 3.46)	0.35
Perennial:Monsoon	-1.5	1.2	(-4, 0.84)	
Moderate Size	1.5	0.6	(0.47, 2.74)	0.29
Large Size	1.7	1	(-0.06, 3.89)	
Riffle Microhabitat	0.1	0.4	(-0.61, 0.93)	0.23
Indeterminate Diapause	-0.3	1.2	(-2.56, 1.88)	0.22
No Diapause	1	1	(-0.97, 2.95)	
Perennial:Indeterminate Diapause	-0.1	1.2	(-2.28, 2.13)	0.16
Perennial:No Diapause	-0.1	1.1	(-2.25, 1.88)	

[†] [**] denotes covariates with strong support (p > 0.7); [*] denotes covariates with some support (p > 0.4)

Table 4.4 Posterior summaries of colonization covariate parameters in the full model (without inclusion parameters) and inclusion probabilities of each parameter.

Parameter	Mean	SD	95% CI	Inclusion Probability[†]
Intercept	-2.8	1.8	(-6.58, 0.6)	-
Perennial Stream	-1	1.3	(-3.44, 1.65)	1.00[**]
Spring Season	1.9	1.3	(-0.65, 4.26)	1.00[**]
Monsoon Season	0.1	1.5	(-2.92, 2.71)	
Perennial:Spring	1.4	1.2	(-0.9, 3.88)	0.84[**]
Perennial:Monsoon	-0.3	1.5	(-3.11, 2.83)	
Indeterminate Diapause	1.8	1.1	(-0.43, 3.83)	0.83[**]
No Diapause	-1.5	1.2	(-3.8, 0.98)	
Active Aquatic Disperser (AAqD)	-0.1	1.5	(-3.04, 2.8)	
Passive Aerial Disperser (PAeD)	0	1.6	(-3.07, 3.19)	0.53[*]
Active Aerial Disperser (AAeD)	-0.3	1.2	(-2.81, 1.93)	
Riffle Microhabitat	-1	0.7	(-2.36, 0.42)	0.37
1 Generation/Year	-1.3	1	(-3.35, 0.62)	0.35
>1 Generation/Year	0.9	1	(-1.23, 2.76)	
Perennial:AAqD	-0.1	1.5	(-3.11, 2.84)	
Perennial:PAeD	0	1.6	(-3.01, 3.03)	0.32
Perennial:AAeD	-0.7	1.2	(-3.22, 1.45)	
WY2011	0.5	1.3	(-1.9, 3.05)	0.30
WY2012	0	1.6	(-3.12, 3.07)	
Perennial:Indeterminate Diapause	1.1	1.1	(-1.08, 3.42)	0.29
Perennial:No Diapause	-0.1	1.2	(-2.56, 2.26)	
Moderate Size	-1.5	1.2	(-3.9, 0.61)	0.17
Large Size	0.7	1	(-1.48, 2.81)	
Perennial:WY2011	0.1	1.3	(-2.43, 2.62)	0.11
Perennial:WY2012	0	1.6	(-3.03, 3.11)	

† [**] denotes covariates with strong support (p > 0.7); [*] denotes covariates with some support (p > 0.4)

Table 4.5 Posterior summaries of detection covariate parameters in the full model (without inclusion parameters) and inclusion probabilities of each parameter.

Parameter	Mean	SD	95% CI	Inclusion Probability[†]
Intercept	-0.4	0.5	(-1.46, 0.55)	-
WY2011	0.5	0.3	(0.04, 1.18)	1.00[**]
WY2012	1.1	0.4	(0.32, 1.95)	
Indeterminate Diapause	-0.1	0.3	(-0.72, 0.66)	0.68[*]
No Diapause	-0.8	0.3	(-1.39, -0.31)	
1 Generation/Year	-0.3	0.1	(-0.53, -0.04)	0.29
>1 Generation/Year	-0.3	0.1	(-0.57, -0.02)	
Riffle Microhabitat	-0.1	0.1	(-0.19, 0.05)	0.07
Perennial Stream	-0.4	0.5	(-1.4, 0.46)	0.06
Active Aquatic Disperser (AAqD)	-1.3	0.6	(-2.59, -0.13)	
Passive Aerial Disperser (PAeD)	0	1.6	(-3.09, 3.19)	0.04
Active Aerial Disperser (AAeD)	-0.3	0.4	(-1.05, 0.39)	
Moderate Size	0.1	0.1	(-0.1, 0.22)	0.02
Large Size	0.1	0.1	(-0.14, 0.28)	
Spring Season	-1.2	0.4	(-1.78, -0.31)	0.01
Monsoon Season	-0.8	0.3	(-1.33, -0.18)	
Perennial:AAqD	1.2	0.6	(-0.06, 2.44)	
Perennial:PAeD	0	1.6	(-3.18, 3.13)	0.00
Perennial:AAeD	0.4	0.4	(-0.27, 1.15)	
Perennial:Indeterminate Diapause	0.2	0.4	(-0.59, 0.88)	0.00
Perennial:No Diapause	0.6	0.3	(0.03, 1.19)	
Perennial:Spring	1.1	0.4	(0.19, 1.7)	0.00
Perennial:Monsoon	0.7	0.3	(0.06, 1.22)	
Perennial:WY2011	-0.2	0.3	(-0.87, 0.29)	0.00
Perennial:WY2012	-0.7	0.4	(-1.61, 0.04)	

[†] [**] denotes covariates with strong support ($p > 0.7$); [*] denotes covariates with some support ($p > 0.4$)

Table 4.6 Posterior summaries of covariate parameters for the median model (covariates with an inclusion probability >0.5). Credible intervals not including zero are bolded.

Process	Parameter	Mean	SD	95% CI
Initial Occupancy	Intercept	2.02	0.67	(0.87,3.49)
	Riffle Microhabitat	-1.06	0.36	**(-1.85,-0.42)**
	Indeterminate Diapause	1.8	0.87	**(0.28,3.69)**
	No Diapause	0.14	0.55	(-1.01,1.13)
Persistence	Intercept	-0.76	0.53	(-1.78,0.33)
	Perennial Stream	4.16	0.38	**(3.46,4.97)**
	WY2011	1.53	0.57	**(0.34,2.65)**
	WY2012	0	1.61	(-3.23,3.12)
	1 Generation/Year	-0.72	0.51	(-1.78,0.19)
	>1 Generation/Year	0.05	0.56	(-1.07,1.04)
	Perennial:WY2011	1.9	1.08	**(0.01,4.05)**
	Perennial:WY2012	0.01	1.58	(-3.11,3.11)
Colonization	Intercept	-0.02	1.09	(-2.03,2.06)
	Perennial Stream	-2.86	0.83	**(-4.53,-1.31)**
	Spring Season	-0.1	0.83	(-1.64,1.57)
	Monsoon Season	2.51	0.93	**(0.85,4.5)**
	Active Aquatic Disperser	-0.17	1.14	(-2.54,2.07)
	Passive Aerial Disperser	0.02	1.59	(-3.12,3.22)
	Active Aerial Disperser	-0.5	0.76	(-2.24,0.87)
	Indeterminate Diapause	1.08	0.67	(-0.18,2.52)
	No Diapause	-0.64	0.51	(-1.59,0.39)
	Perennial:Spring	1.63	1.19	(-1.26,3.7)
	Perennial:Monsoon	-1.72	1.16	(-4.06,0.44)
Detection	Intercept	-1.01	0.1	(-1.22,-0.81)
	WY2011	0.29	0.06	**(0.16,0.41)**
	WY2012	0.4	0.08	**(0.25,0.55)**
	Indeterminate Diapause	-0.07	0.11	(-0.28,0.15)
	No Diapause	-0.26	0.1	**(-0.45,-0.07)**
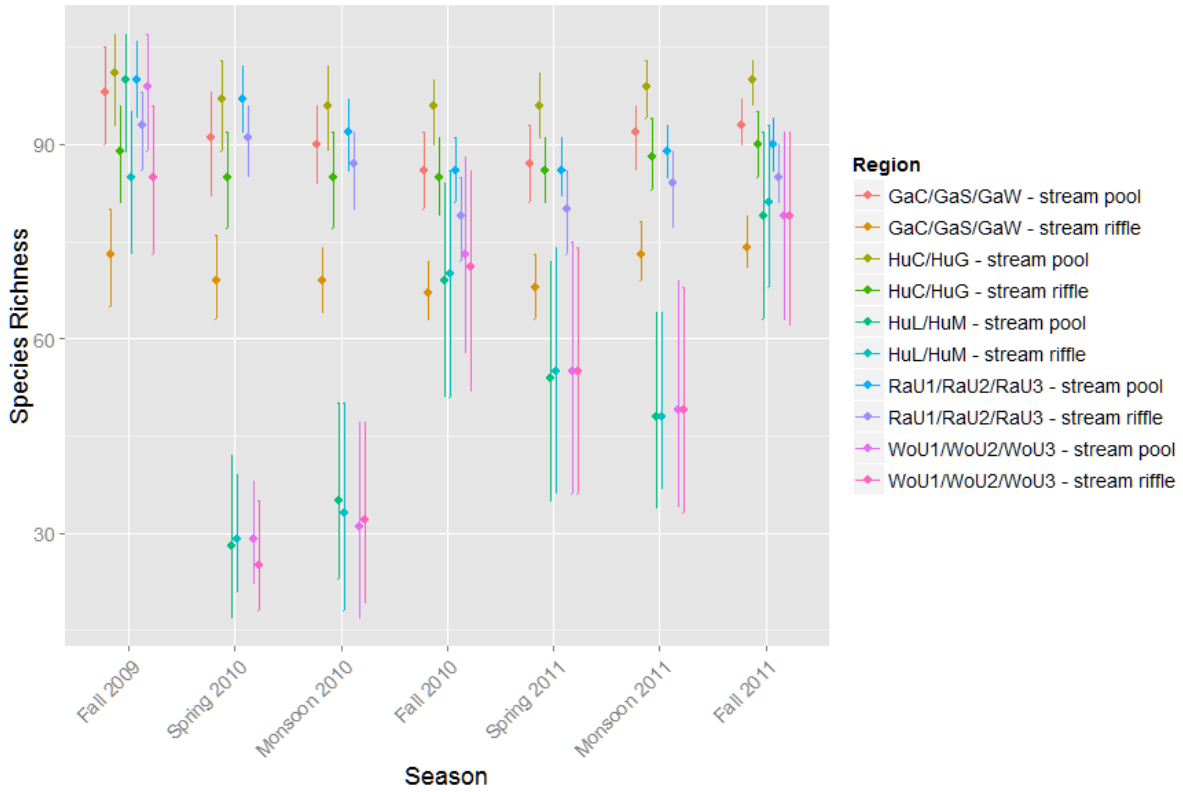
Figure 4.3 Median species richness of focal invertebrates in each region per sampling season, as indicated by the selected median model. Error bars represent 95% credible intervals on biodiversity estimates.

5 Neutral models demonstrate the effect of spatial configuration of habitat capacity on β diversity

Synopsis: This chapter uses a neutral modeling approach to demonstrate that well-known biodiversity metrics can be misleading or wrong when looking across habitats that vary significantly in size or "habitat capacity." In addition to being important to the field of biodiversity studies, this study is important for managers because it shows how habitat size can have a strong influence on the biodiversity present at specific sites within a system.

5.1 Abstract

Patterns of β diversity are commonly used to infer underlying ecological processes. In this study, we examined the effect of spatial configuration of habitat capacity on different metrics of β diversity, i.e., β diversity as turnover and as variation. For β diversity as turnover, a monotonic species spatial turnover pattern is typically considered a benchmark for species distributions only controlled by dispersal, deviations from which are attributed to local environmental filtering (the situation in which the same environmental factors affect different species differently). However, we found that spatial configuration of habitat capacity causes non-monotonicity in species spatial turnover. After applying a recent null-model approach—designed to tease out the effect of variation in α diversity induced by the spatial configuration—species spatial turnover remained non-monotonic. This non-monotonicity makes it difficult to distinguish between the deterministic environmental filtering and stochastic dispersal processes based on the pattern of species spatial turnover. Spatial configuration of habitat capacity also influences landscape connectivity: with the same total habitat capacity, a landscape where the small-habitat capacity sites are located in the middle may constrain species movements between sites at the opposite ends of the landscape (akin to a bottleneck effect or fragmentation). This results in higher spatial variation of species composition, hence, higher β diversity as variation. Ecologists who use different measures of β diversity should be aware of these effects introduced by spatial configuration of habitat capacities.

5.2 Introduction

A burgeoning challenge in ecology is to distinguish among the many dimensions of species diversity. Increased scientific activity has centered on the study of beta (β) diversity – broadly defined as the variation in species membership among locales – because it provides a direct link between local biodiversity (α diversity) and regional species pool (γ diversity) (Whittaker 1960; Whittaker 1972) and it has numerous implications for conservation (Olden 2006). Ecologists frequently use β diversity to infer processes that structure species assemblages spatially (Vellend 2010). However, landscape heterogeneity, one aspect of which is manifested as spatial variation in habitat capacity (defined as the potential number of individuals a site can hold) among sites, can make it difficult to infer processes from observed β diversity patterns. Variation in habitat capacity introduces, among other things, differences in α diversity among sites via the simple

effect of random sampling. As a result, variation in α diversity can generate spurious similarities or differences between locales, i.e., β diversity (Lennon et al. 2001; Koleff et al. 2003; Baselga 2007; Chase et al. 2011).

Beta diversity is expressed both in terms of species turnover and variation (Anderson et al. 2011). Species turnover refers to the rate of change in community structure along a given gradient, such as the distance decay relationship (DDR) describing decreasing taxonomic similarity with geographic distance (e.g., Qian and Ricklefs 2007; Brown and Swan 2010). Ecologists expect monotonic decay of species spatial turnover to occur when a system is predominantly controlled by dispersal limitation, whereas deviations from DDR (i.e., "peaks" and "valleys" in the species spatial turnover) indicate the importance of local environmental filtering on species occurrence (e.g., Condit et al. 2002; Anderson et al. 2013; Bogan et al. 2013). β diversity as represented by Whittaker's original measures of β diversity reflects the variation in species identities among units ($\beta_w = \gamma / \overline{\alpha}$) or the mean dissimilarity index (such as Bray-Curtis and Sorensen dissimilarity index) among communities (

$$\bar{d} = \frac{1}{m} \sum_{i,j<i} d_{ij}$$

, $m = N(N-1)/2$, N is total sample units) (Anderson et al., 2013). Greater values indicate higher variation in species composition across space. In this study, we examine how the validity of the inferences about ecological processes based on different measures of β diversity may be compromised by the spatial configuration of habitat capacity in a landscape. We define spatial configuration of habitat capacity (hereafter SCHC) as the spatial arrangement of sites with different habitat capacities in a landscape. We examined this effect by fixing the total habitat capacity of all the sites and varying the spatial arrangements of them.

Various methods exist to correct for the effects of α diversity on estimates of β diversity. It should be noted that these effects relate to the dependence of β diversity on the differences of α diversity *between sites within a system*, *not* the differences of the mean α diversity—*i.e., averaged across all sites within a system*—among different systems. The latter issue is related to the comparability of β diversity measures among systems with different mean α diversity, and has been addressed by several authors (e.g., Jost 2007; Jost et al. 2010; Baselga 2010). Our study addresses the first issue: the dependence of β diversity on the differences of α diversity between sites within a system (e.g., Lennon et al. 2001; Koleff et al. 2003; Baselga 2007). Chase et al. (2011) recently developed a null-model approach, originally proposed by Raup and Crick (1979), to detect whether different species compositions among sites result from differences in diversity or from other ecological processes (e.g., deterministic environmental filtering and stochastic dispersal). However, this approach was developed for a pair of local communities, and its effectiveness and validity when applied to all pairwise combinations of communities in a landscape have not yet been systematically explored.

Spatial configuration of habitat capacity also influences landscape connectivity. For example, low capacity habitats in the landscape matrix may constrain movements (i.e., dispersal) between

locations supporting high capacity habitats. Greater connectivity among habitats allows immigration from others sites to offset local extinction events, leading to higher α diversity but lower variability in community composition across the landscape (i.e., lower β diversity). By contrast, lower connectivity can isolate habitats leading to lower α diversity but higher species turnover (i.e., higher β diversity) (Hubbell 2001; Economo and Keitt 2010; Carrara et al. 2014). Although the influence of landscape connectivity for community composition is widely appreciated (Chase and Ryberg 2004; Chave and Norden 2007; Minor et al. 2009), few studies have considered the sole effects of habitat spatial configuration on β diversity.

In this paper, we examine how the quantification and interpretation of β diversity patterns are influenced by the spatial configuration of habitat capacity (hereafter SCHC, defined as the arrangement of local communities with different habitat capacities in a landscape). Addressing this question through the analysis of empirical data is challenging because many known and unknown ecological processes are in operation. Therefore, we examined the effects of SCHC on β diversity patterns using simulated landscapes that are free from the effects of environmental filtering. A set of communities comprised a metacommunity on this landscape, and we assumed that the locales that supported the communities differed only in their habitat capacity. As a result, species distributions—and the corresponding β diversity patterns—would be controlled solely by dispersal and not by differences in the ecological niche requirements of species.

The SCHC gives rise to spatial variation in α diversity, which subsequently affects β diversity patterns (Lennon et al. 2001; Koleff et al. 2003; Baselga 2007; Chase et al. 2011). If the influence of α diversity is effectively removed, β diversity patterns should have the following properties in the hypothetical landscape free from the effect of environmental filtering (Figure 5.1). First, β diversity as turnover should conform to the monotonic decay relationship describing how species similarity decreases with spatial distance. Second, β diversity, measured as either turnover or variation, should be statistically indistinguishable across landscapes with different spatial configurations of habitat capacities. Although these two predictions may appear intuitive, it is unclear whether frequently used β diversity measures conform to these properties. We systematically investigated the effects of SCHC on the robustness of these two properties by implementing a neutral metacommunity model (see, e.g., Hubbell 2001 and Muneepeerakul et al. 2008) in the no-niche hypothetical landscape described above.

Spatial configuration of habitat capacity (SCHC)

introduces

introduces

Variation in alpha diversity within a metacommunity

Variation in landscape connectivity across metacommunities

| H1 | H2 | H3 | H4 | H5 |

| H1' | H2' | H3' | H4' | H5' | System 1 |

| H1" | H2" | H3" | H4" | H5" | System 2 |

Expected Pattern:

Expected Pattern:

Observed Pattern: non-monotonic

Observed Pattern: Difference in β diversity caused by difference in landscape connectivity in two systems

Figure 5.1 Schematic representation of the effect of spatial configuration of habitat capacity (SCHC) on β diversity - testing the validity of the two properties of β diversity when the metacommunity is controlled only by dispersal.

5.3 Methods

We systematically investigated the effects of SCHC on estimates of β diversity by applying a neutral metacommunity model (Muneepeerakul et al. 2008) in one-dimension (e.g., such as a stream) with different spatial configurations of habitat capacity (Figure 5.2). In the "uniform" configuration, each habitat had identical habitat capacity. In the "gradient" configuration, habitat capacity increased linearly along a hypothetical gradient. In the "random-shuffle" configuration, we randomized the spatial distribution of habitat capacities along the gradient. In the "V-shaped" configuration, habitat capacity was set high at both ends and low in the middle of the gradient; this is akin to a stream system in which the headwater receives much rainfall and the downstream end connects to a large river, while the middle reaches are intermittent streams (e.g., Bogan et al. 2013). In the "hump-shaped" configuration, habitat capacity was large in the middle and small at the two extremes of the gradient—akin to an edge effect such as the boundaries of a forest experiencing more external pressure than its interior. All five configurations had the same average habitat-capacity size of 514, and thus the same total habitat capacity. All configurations except for the uniform configuration were built from the same set of habitat capacities, but they were configured differently in space (Figure 5.2). The biggest sample-size discrepancy (i.e., ratio of largest to smallest habitat capacity) in the four non-uniform configurations was about 20.
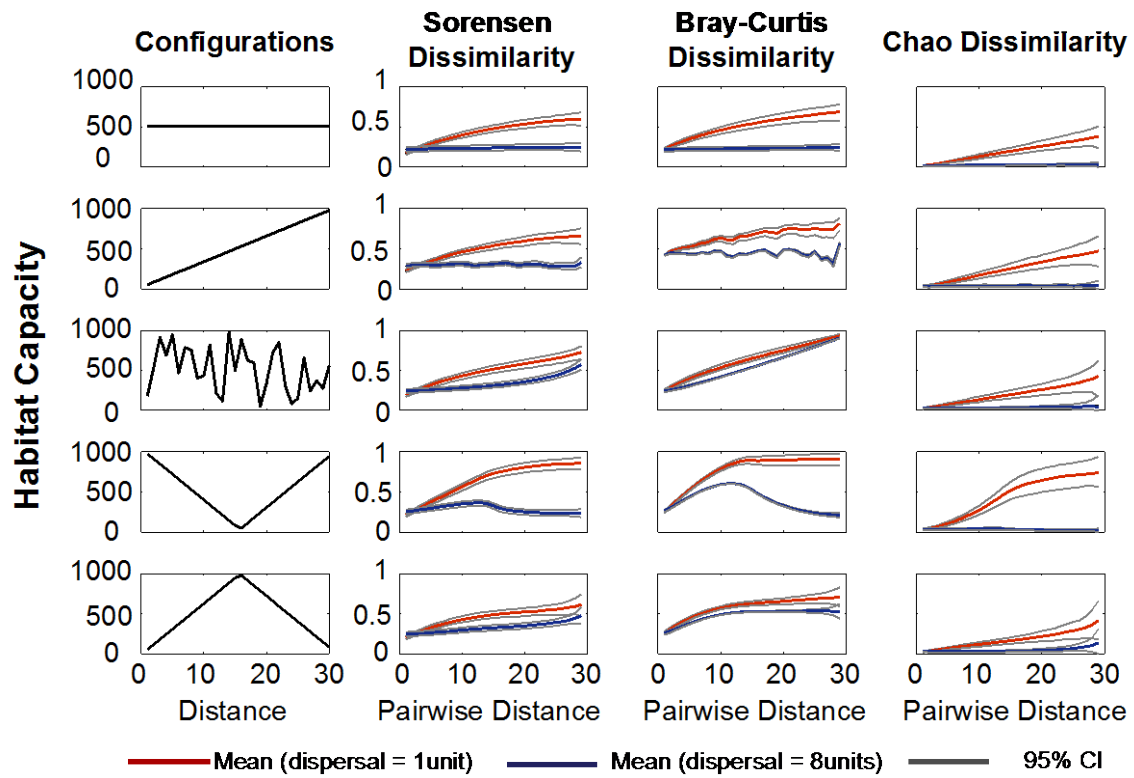
Figure 5.2 The effect of spatial configuration of habitat capacity (SCHC) on species spatial turnover at two levels of dispersal limitation (solid red line: 1 distance-unit; solid blue line: 8 distance-units).

The metacommunity consisted of 30 local communities, with a distance between neighboring sites of 1 arbitrary distance unit. The dispersal kernel was assumed to be a two-sided exponential distribution:

$$K_{ij} = Ce^{-L_{ij}/a}$$

where K_{ij} is the probability that an organism produced at site j arrives at site i after dispersal; C is a normalization constant to ensure that for every site j, $\sum_i K_{ij} = 1$, i.e., no organisms traveled out of the metacommunity. L_{ij} is the distance between two habitats, and a was the characteristic dispersal distance. At each time step, a randomly selected individual died and the resources that previously sustained that individual became available to sustain a new individual. With probability v, the diversification rate, the empty spot was taken up by a new species (the diversification rate is a per-birth rate and is due to speciation or to immigration of a new species from outside the metacommunity). With probability 1-v, the empty spot was occupied by a species already existing in the system. In the latter case, the probability P_{ij} that the empty spot in site i would be colonized by a species from habitat j was determined as follows:

$$P_{ij} = (1 - v) \frac{K_{ij} H_j}{\sum_{k=1}^{N} K_{ik} H_k}$$

where K_{ij} is the dispersal kernel, H_k is the habitat capacity of site k, and N is the total number of sites (i.e., communities). All the organisms in site j had the same probability of colonizing the empty spot at site i where the death took place. Each site was assumed to be always saturated at its habitat capacity.

We explored five characteristic dispersal distances ($a = 1, 4, 8, 12, 16$) at the diversification rate $v = 0.0010$. In the metacommunity's initial state, the distribution of species composition was random. No environmental filtering was present. We ran the model until it reached a statistically steady state (when there is no directional trend in the mean α diversity or total species richness with simulation time steps).

Results from the neutral metacommunity model were used to calculate different β diversity measures. Three commonly-used measures of β diversity were considered: species presence/absence according to Sorensen dissimilarity index, species abundance according to Bray-Curtis dissimilarity index, and species abundance according to the more recent Chao-Sorensen dissimilarity index (Chao et al. 2005), which was originally created to address the issue of under-sampling rare species.

To control for the effect of variation in α diversity, we applied Chase et al.'s (2011) null-model approach to calculate pairwise β_{RC}. The β_{RC} metric expresses the magnitudes by which

communities deviate from a stochastic null expectation. β_{RC} uses a randomization approach to estimate the probability to which pairwise communities have less observed number of shared species between community 1 and 2, containing α_1 and α_2 species, given repeated random draws of α_1 and α_2 species from a known species pool. It does so by comparing SS_{obs} with the distribution of SS_{exp}—the expected number of shared species from random draws. β_{RC} therefore calculates the probability that SS_{obs} is lower than SS_{exp} by chance (i.e., a dissimilarity index).

We used the four pairwise dissimilarity indices described above to calculate β diversity as turnover and as variation (Anderson et al. 2011). For β diversity as turnover, we used the slope between pairwise species similarity and pairwise geographical distance as a direct measure of turnover (e.g., Qian and Ricklefs 2007). We also considered the relative strength of the relationship (r^2) between species similarity and distance, as recommended by Anderson et al. (2013). For β diversity as variation, we considered the classic metrics of β diversity, including Whittaker's proportional β diversity ($\beta_W = \gamma / \overline{\alpha}$) and the additive model of β ($\beta_{Add} = \gamma - \overline{\alpha}$) (Lande 1996; Crist and Veech 2006), as well as multivariate measures of β diversity (i.e., the mean of the pairwise dissimilarity indices), which are based on pairwise resemblance of species among habitats (Anderson et al. 2013). Since the classic β diversity is directly derived from α and γ diversity, we investigated the effects of SCHC on α and γ diversity as well.

5.4 Results

SCHC introduces non-monotonicity to species spatial turnover. By design, a neutral metacommunity model is free from the effects of environmental filtering, and thus patterns of spatial species turnover are shaped solely by stochastic dispersal. Therefore, we expect monotonic decay in species similarity with pairwise distance; however, we found little evidence for this relationship (Figure 5.2). Species turnover was non-monotonic when measured by the traditional presence/absence-based Sorensen index and the abundance-based Bray-Curtis index. Chao index, however, showed less evidence for non-monotonicity in species spatial turnover across different configurations. The non-monotonicity observed was caused by the variation in α diversity among the communities induced by the SCHC.

The null model approach is not effective in separating α from β diversity. Next, we tested the hypothesis that the observed non-monotonicity in species turnover is caused by variation in α diversity. We first tested the effectiveness of Chase et al.'s (2011) method to disentangle α from β diversity in spatially explicit context, using a randomly assembled metacommunity without dispersal limitation. The dispersal-free metacommunities were created by randomly selecting species from a common pool of a given regional diversity ($\gamma = 200$). Each species had the same probability of being selected and was assigned to local communities until the local habitat capacity was reached. The random assembly of species was repeated 500 times for each configuration. Our results demonstrated two main findings. First, the mean pairwise similarity across 500 realizations was 0, indicating no difference from a random assemblage (Chase et al. 2011). Second, the slope of turnover curve was 0, with an intercept of 0 (Figure 5.3). These

results suggest that the Chase et al. (2011) method was effective under random species assemblages. It is worth noting that the confidence intervals were of varying widths, but all were wide.
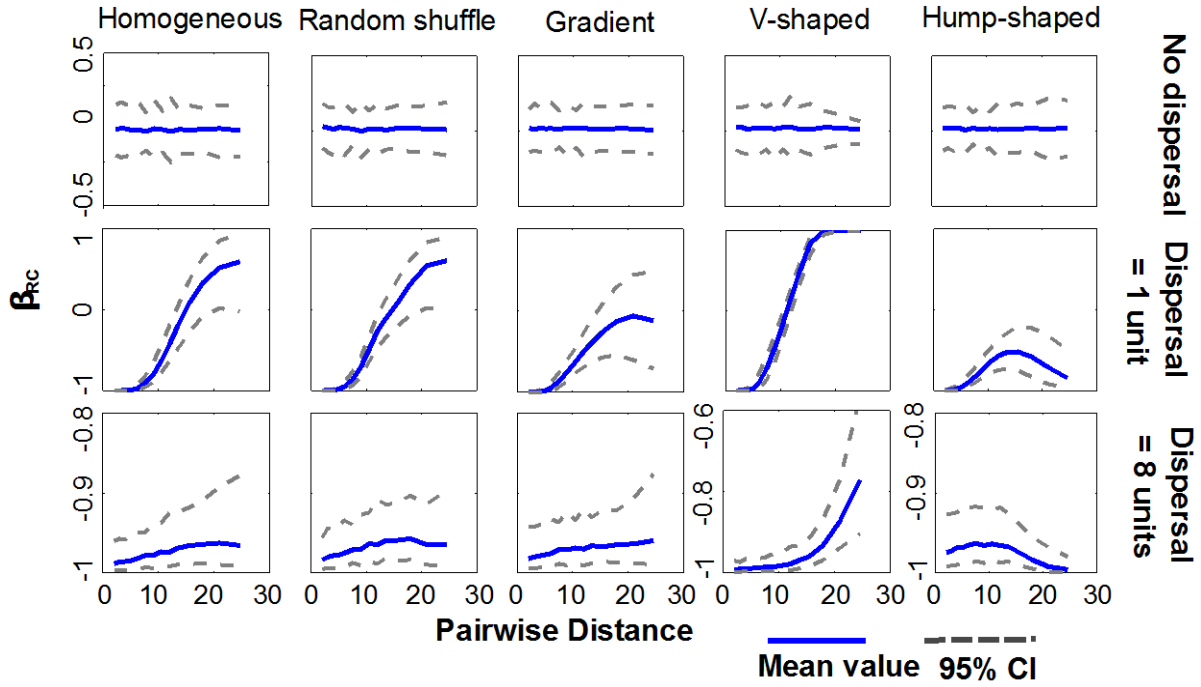
Figure 5.3 Patterns of β_{RC} at different levels of dispersal (γ diversity = ~200). When the community is assembled randomly, the mean of β_{RC} (blue solid line) is at 0, the width of the $5^{th} - 95^{th}$ percentile envelope (gray dashed line, created with 500 replicates) is wide, and the envelope changes with the pairwise distance in the V-shaped and hump-shaped configurations. When dispersal is introduced, the change in the $5^{th} - 95^{th}$ percentile envelope with pairwise distance is more obvious. We observed non-monotonicity in the hump-shaped configuration (at both dispersal levels) and the gradient configuration (when dispersal = 1 unit). (If there exists a mean of β_{RC} at larger pairwise distances statistically lower (Welch-Satterthwaite t test; $p < 0.01$) than a mean β_{RC} at smaller pairwise distance, it is considered to be non-monotonic.)

We then included dispersal limitation in creating metacommunities at landscapes of different SCHCs, and expected that β_{RC} would exhibit a monotonically increasing pattern in all configurations. Contrary to our expectation, in the hump-shaped and gradient configurations, we found that species turnover was non-monotonic (Figure 5.3). We also found that the confidence interval generally became wider with increasing pairwise distance. Despite the widening confidence intervals, the non-monotonicity in species turnover curve was still statistically significant.

SCHC causes differences in β diversity across metacommunities. We assessed the effect of SCHC on β diversity across metacommunities to determine whether, after the effect of α diversity is removed, β diversity is statistically indistinguishable across landscapes with different spatial configurations of habitat capacities. To do this, we examined both types of β diversity: turnover and variation (Anderson et al. 2011).

We found that the slope between similarity and geographical distance differed among varying configurations of the landscape, and Chao index and β_{RC} did not conform to the linear models (i.e., very low r^2 values when the relationship was non-monotonic).

The examination of β diversity as variation found that Whittaker's β_W and Lande's β_{Add} were influenced by SCHC (Table 5.1; Figure 5.4). Mean pairwise dissimilarity indices were also significantly different across configurations. Higher values were found in the V-shaped configuration and lower values in the hump-shaped configuration. We also found that SCHC caused differences among metacommunities in both mean α diversity and γ diversity, especially in mean α diversity. Mean α diversity was much higher in the hump-shaped configuration than in the V-shaped configuration. By contrast, mean γ diversity was slightly lower in the hump-shaped configuration than in the V-shaped configuration.

Table 5.1 Effects of the spatial configuration of habitat capacity (SCHC) on β-diversity according to β-diversity variation, mean α diversity, and γ diversity at two levels of hypothetical dispersal. Effects are greater when dispersal level is more local. F (3, 1996) ratio is several magnitudes greater for multivariate measures of β with a characteristic dispersal distance of 1 unit compared to a distance of 8 units. The difference also exists for classic measures of β, α, and γ, but it is not as evident. Variation is calculated as the average of similarity index calculated among all pairs of communities for each non-homogenous configuration (i.e., gradient, random-shuffle, V-shaped, and hump-shaped configurations). For each configuration, 500 replicates (i.e., 500 realizations of the neutral metacommunity model) were used. (γ diversity = ~200). The smallest F value was 6.3, when $p = 0.003$. All other F values were much more significant.

	Multivariate measure of β as variation	Classic measure of β	α and γ

Index	Sorensen Index	Bray-Curtis Index	Chao-Sorensen Index	β_{RC}	β_{Add}	β_W	Mean α	γ
1-unit disp.	4806.4	9822.0	5357.1	7366.6	194.7	3330.3	2509.6	76.5
8-unit disp.	13.8	89.5	6.3	194.8	130.0	1387.0	1158.0	45.7
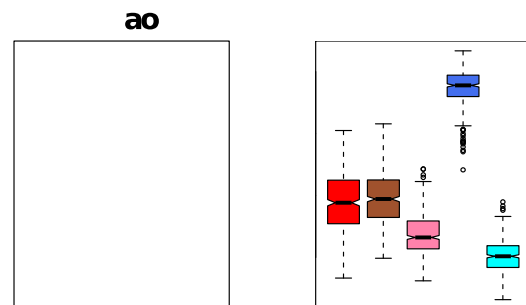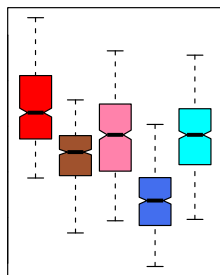
Figure 5.4 The influence of SCHC on β diversity as variation, measured with classic metrics of species diversity (mean α, γ, β_{Add}, and β_W) and mean of dissimilarity indices (Sorensen dissimilarity index (SDI), Bray-Curtis dissimilarity index (BCI), Chao dissimilarity index, and β_{RC}). The results were based on 500 realizations of the neutral metacommunity model with a characteristic dispersal distance of 1 unit.

Dispersal limitation changes the effect of SCHC. We examined two effects of SCHC: (1) its effect on the shape of species turnover curve, and (2) its effect on β diversity, both as variation and turnover, across metacommunities. Both effects varied with the strength of dispersal limitation. Non-monotonicity was more evident when dispersal was more widespread according to the three traditional indices. For β_{RC}, which corrects for α diversity variation, SCHC had greater effects on the shape of species turnover when dispersal was more local. When dispersal limitation was absent, the shape of species turnover across different configurations was similar , suggesting little effect of SCHC. In terms of SCHC's effect on β diversity across metacommunities, the influence of SCHC was more pronounced when dispersal was more local, i.e., the difference in β diversity among metacommunities caused by SCHC is amplified when the dispersal was more local. We explored five levels of dispersal limitation, but only reported result for two; the patterns reported here hold for the rest three dispersal levels.

5.5   Discussion

The interdependence of β and variation in α diversity is well established in the literature (e.g., Koleff et al. 2003; Jost 2007; Chase et al. 2011). One contribution of our study is to examine how the variation in α diversity may affect different measures of β diversity in spatially explicit context. Such variation is induced by the SCHC. We found that traditional similarity indices, be they incidence- or abundance-based were highly sensitive to the SCHC. Even with only dispersal limitation in place, patterns of species turnover measured by these indices were non-monotonic. Non-monotonicity, such as "peaks," "valleys," and "plateaus" (e.g., Condit et al. 2002; Anderson et al. 2013; Bogan et al. 2013), in species spatial turnover has been used as evidence for local processes shaping community composition at certain distances. We did not observe non-monotonicity in the species spatial turnover measured by Chao index. Our findings imply that, when local habitat capacities in the landscape are not uniform (a common occurrence), analyses of spatial turnover based on these frequently used similarity indices should be interpreted with care because they are at risk of inadvertently conflating ecological processes with confounding effect by α diversity in their conclusions.

The methods available to remove the influence of α diversity variation seem ineffective for the β diversity patterns discussed here. For example, Chase et al.'s (2011) null-model approach, which was designed to correct for the effect of variation in α diversity on β diversity, is useful for deciding whether the community assemblage is significantly different from a random assemblage. But it was developed for a single community pair; our results show that it is not readily transferable for comparisons among all pairs. Nonetheless, β_{RC} has already been applied at landscape scales in many very recent studies (e.g., Akasaka and Takamura 2012; Bernard-Verdier et al. 2012; Anderson et al. 2013; Siepielski and McPeek 2013).

Why can't β_{RC} be extended to more than one pair? The calculation of β_{RC} is based on comparing the value of SS_{obs} with the probability density distribution of SS_{exp}. The probability density

distribution of SS_{exp} is generated by repeated random sampling for a pair of communities with a given α diversity level. Inevitably, α diversity levels vary across different community pairs. Different α diversity combinations result in different shapes of the SS_{exp} distribution (i.e., skewedness and variance) (Chase et al. 2011). Variation in the shape of SS_{exp} distribution makes comparison among different pairs problematic.

To see this, we note that $β_{RC}$ is highly sensitive to SS_{obs}. When SS_{obs} falls near the peak of SS_{exp} distribution, a small change in the value of SS_{obs} results in a disproportionally large change in the value of $β_{RC}$ (see Figure 5.5 and its caption for an example)—even a change in its sign. In reality, under-sampling of rare species could easily result in such small fluctuations in the value of SS_{obs} collected in the field. Therefore, absolute values of $β_{RC}$ are not reliable for inferring underlying ecological processes. Now, to demonstrate problems in the context of species spatial turnover, we took two pairs of communities in the hump-shaped configuration as an example (Figure 5.6). The first pair consists of the two communities at both ends (i.e., communities 1 and 30), and the second pair consists of communities 12 and 18, which are much closer to each other than the first pair. After removing the effect of variation in α diversity, we expected the second pair to be more similar in species composition, i.e., having a lower $β_{RC}$; instead, it was less similar. Accordingly, this could lead to an interpretation that ecological processes other than dispersal are at play where there is none.
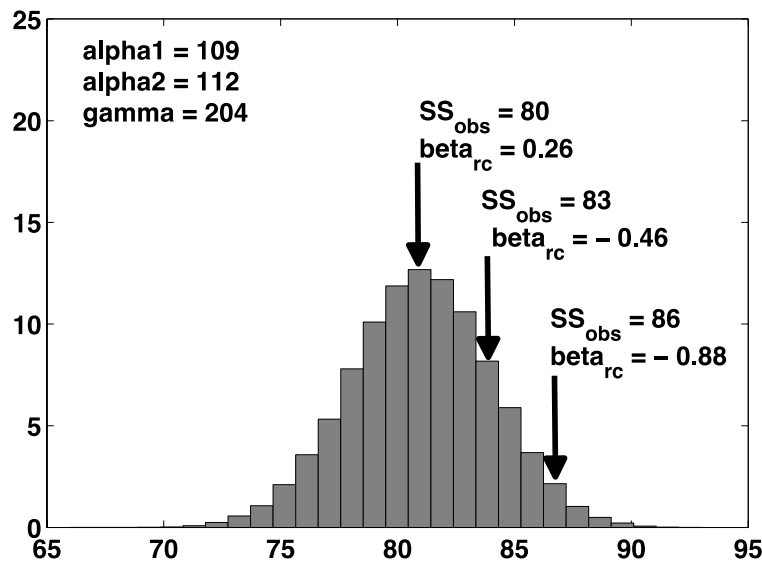
Figure 5.5 $β_{RC}$ is very sensitive to small changes in observed shared species (SS_{obs}) when the value of SS_{obs} falls within or near the peak of SS_{exp} distribution. SS_{exp} distribution was created by 99,999 repeated random draws of $α_1$ and $α_2$ species from a known species pool. The γ diversity of 204 was taken from one of the neutral metacommunity model realizations in the V-shaped configuration, with dispersal = 8 units.

In the pair of communities at both ends (i.e., community 1 and 30), $\alpha_1 = 109$, $\alpha_2 = 112$, and $SS_{obs} = 83$. Small changes in the value of SS_{obs} led to a change in sign of β_{RC} (e.g., decreasing the number of shared species by 3 resulted in $\beta_{RC} = 0.26$). Positive and negative values have totally different ecological interpretations.
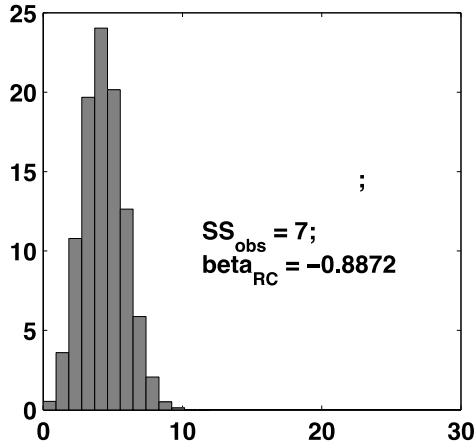
Figure 5.6 The shape of SS_{exp} distribution influences β_{RC}. Red bars indicate the number of observed shared species.

Another reason that SCHC causes complications in interpreting β diversity patterns is the spatial autocorrelation between the SCHC and dispersal. It is useful to see this through a lens of the effects of variation in habitat capacity. The variation in habitat capacity affects patterns of spatial turnover in two ways. First is a random sampling effect: if the overall species richness is fixed, two habitats with larger and more equal carrying capacity are likely to have a greater proportion of common species, hence a higher similarity value. Second is the spatial correlation between SCHC and dispersal. Corrective methods such as null-model shuffling (Kraft et al. 2011) effectively remove the random sampling effect, but not the spatial autocorrelation effect. Therefore, the effectiveness of these methods depends on species' dispersal capacity, which is difficult to estimate in reality.

Another contribute of our study was that we confirmed the effect of SCHC on β diversity via its effect on landscape conductivity. The hump-shaped landscape and V-shaped landscape have same total habitat capacity; however, in the V-shaped landscape, the sites with lower habitat capacity level are located in the center of the landscape, and they are located on the edge of the landscape in the hump-shaped landscape. Smaller habitat capacity in the center of the landscape greatly reduces landscape connectivity, and increases isolation among sites. As a result, the local species diversity is low (low mean α diversity), but the species composition is more spatially variable, i.e., higher β diversity. By fixing the overall landscape carrying capacity, and only

changing the spatial arrangement of habitats of different size, we demonstrated the significant effect of SCHC on different measures of β diversity. This mechanism is often neglected in interpreting β diversity patterns.

As the upshot of our investigation, we recommend that for ecologists who wish to use the shape of species spatial turnover to infer underlying ecological processes, Chao index is currently the best choice. According to our study, Chao index is considerably more robust than traditional similarity indices: it exhibits no or very weak non-monotonicity when only dispersal limitation is present. One possible explanation for this robustness is that SCHC influences spatial patterns of rare species, and the Chao index was already designed to minimize sensitivity to rare species (Chao et al. 2005). That said, the Chao index is not completely insensitive to the SCHC effects. Our findings suggest that when inferring ecological explanations from β diversity patterns, researchers should take into account not only the commonly considered deterministic and stochastic processes (e.g., species adaption to habitat quality, dispersal, extinction, and speciation), but also the effects of spatial configuration of habitat capacities, which alters patterns of β diversity by introducing variation in α diversity and influencing landscape connectivity, which further influences dispersal limitation and other spatial processes.

5.6   Acknowledgements

6 Importance of neutral processes varies in time and space: evidence from dryland stream ecosystems

Synopsis: This chapter uses a neutral model approach to understand how our invertebrate biodiversity dataset is affected by factors such as season, year, and precipitation. In general, the study found that neutral biodiversity processes were most important during extremely high and low flow periods, but niche processes dominated in moderate flow periods.

6.1 Abstract

Many ecosystems experience strong temporal variability in environmental conditions. Although temporal variability is important for understanding community structure, a clear picture of how niche and neutral processes operate in temporally variable systems remains elusive. In this paper, we used neutral metacommunity models to analyze macroinvertebrate community data spanning multiple seasons and years from 20 sites in a Sonoran Desert river network in Arizona, U.S.A. Averaging over eight stream flow conditions across three years, we found that neutral processes were more important in perennial streams than in non-perennial ones. Averaging across perennial and non-perennial streams, we found that neutral processes were more important when streams were in very high flow and very low flow periods (i.e., with drying and flooding of high severity), while the effect of niche processes peaked in intermediate or normative flow conditions. These findings were robust to the choice of model parameter values. Our study suggested the possibility that the net effect of disturbance on both niche and neutral processes depends on its severity. This is in contrary to the prevailing understanding that disturbance promotes niche processes. We argue that neutral processes could be triggered again when the severity of disturbance is beyond a certain threshold such that all organisms are adversely affected regardless of their biological traits and strategies. The notion that neutral and niche processes are competing hypotheses in community ecology should be replaced with the notion that these processes operate simultaneously, with their relative strengths changing in space and time.

6.2 Introduction

Understanding community assembly – what processes dominate the spatial and temporal patterns of biodiversity – is a long-standing question in community ecology (Rosenzweig 1995). In particular, the discussion on the relative importance of niche *vs.* neutral processes has often taken a dichotomous stance (Harpole and Tilman 2006; McGill et al. 2006). In the niche view, all species differ from each other, and their distribution and abundance are limited by a set of factors: physical habitats selects species with suitable biological traits and filters out other species in the regional species pool (i.e., deterministic processes) (Gause 1934). The neutral view, in contrast, referring to lottery dynamics (i.e., stochastic processes), operates on the assumption that these interspecific differences are immaterial for certain biodiversity patterns (Hubbell 2001).

Environmental disturbance is an important force driving community structure and dynamics, and its effects have received considerable attention in the community ecology literature (Poff and Ward 1989; Urban 2004; Gouhier et al. 2010). Both experimental evidence and theory have suggested that environmental disturbance can influence community assembly (Jiang and Patel 2008; Lepori and Malmqvist 2009; Vergnon, Dulvy and Freckleton 2009; Stokes and Archer 2010), including the relative importance of niche and neutral processes. Exactly how disturbance influences such relative importance, however, is still open to debate. Several studies, for example, seem to support the hypothesis that neutral processes dominate in places with stable environment, whereas harsh environments with stronger disturbances lead to niche selection by filtering out species lacking the traits to adapt to disturbances (e.g., Inouye and Tilman 1995; Chase 2003; Trexler et al. 2005; Chase 2007). Other studies, however, suggest a more complex, non-monotonic relationship. For instance, Lepori and Malmqvist (2009) surveyed 17 streams in North Sweden featured with different severity of floods in otherwise similar physical background, and found that the strength of niche processes increased with the severity of flood disturbance initially, but weakened once the severity is beyond a certain intermediate threshold. These findings lend support to an alternative hypothesis that neutral processes can be also important under very severe disturbances, presumably because these disturbances cause random extinction and random recolonization even for those organisms most resistant to disturbance. Findings in this present study will contribute to this debate.

Dryland streams are known for their environmental temporal variability, existing in a precarious balance between drying disturbance and flooding disturbance (Datry et al. 2015). They are also highly heterogeneous in space of stream flow, consisting of a mix of perennial, intermittent, and ephemeral streams varying greatly in flow permanence and flow duration (Stanley et al. 1997). While all these stream types experience flood disturbance, intermittent and ephemeral streams suffer from the additional drying disturbance. Therefore, dryland streams are an appropriate system to assess the effect of environmental disturbances on the relative strength of niche and neutral processes. Indeed, considerable amount of literature has shown that aquatic invertebrate community in dryland streams is strongly influenced by hydrological regimes and flow spatial heterogeneity (Lytle and Poff 2004; Bogan and Lytle 2011; Bogan et al. 2013). In these systems, the role of niche processes (environmental filtering imposed by hydrological regime) has been well documented (e.g., Bogan et al. 2013; Schriever et al. 2015; Cañedo-Argüelles et al. 2015; Leigh and Datry 2016), yet it remains unclear whether neutral processes may also play a role and how this role varies in space (along the gradient of harshness: perennial vs. non-perennial streams) and in time (the system undergoing different disturbance types of different degrees of severity over time: drying, intermediate flood, large flood etc.).

In particular, we will address the following two questions: (1) are neutral processes more important in perennial streams or non-perennial ones? And (2) does the community assembly processes change with flow variation (which is correlated with different types of disturbance – drying and flood, and intensity of disturbance) in time and how? To address these questions, we

analyzed macroinvertebrate community data spanning multiple seasons and years from 20 sites in a Sonoran Desert river network in Arizona, U.S.A., and built spatially- and temporally-explicit neutral metacommunity models to assess the changes of relative importance of neutral processes in space and in time.

6.3   Methods

We incorporated temporal variability at two time scales (intra- and inter-annual) in spatially explicit neutral metacommunity models and compared the model performance under different settings to determine the contribution by neutral processes. The rationale commonly used to infer the relative importance of niche and neutral processes in different environments (e.g., harsh vs. benign environment, before vs. after disturbance) is based on β diversity (e.g., Chase 2007; Lepori and Malmqvist 2009; Chase and Myers 2011; Ferrenberg et al. 2013; Ferrenberg et al. 2016): when the observed site-to-site similarity (β diversity) is not significantly different from the null model, the metacommunity is dominated by stochastic neutral processes; if the observed β diversity is significantly lower than the null model approach, niche processes are dominant. The null model approach, although designed to avoid bias caused by variation in α diversity, has been shown to be problematic (Dong et al. 2015) and the framework for using β diversity to differentiate between niche and neutral mechanisms is not robust (Tucker et al. 2016). Here we used a more intuitive method, which involved fitting the metacommunity under different environmental conditions to neutral metacommunity models with different temporal patterns implemented, and then comparing the model goodness of fit. We interpreted the model goodness-of-fit as the explanatory power of neutral processes (as in Stokes and Archer 2010). For example, if the model goodness-of-fit for perennial is better than that for non-perennial streams, we interpret that as the relative importance of neutral processes being greater in perennial streams compared to non-perennial ones.

Site and climate description. The study region included headwater streams of the San Pedro River located in the Sonoran Desert of southeastern Arizona, U.S.A. (Figure 1.1Figure 6.1). Mean annual precipitation in the region is approximately 35 cm, but is highly variable from year to year. Within a year, precipitation is strongly bimodal, with roughly 60% of precipitation occurring during brief, intense summer (July-September) monsoon storms and 40% during more prolonged, moderate-intensity winter (December-April) storms.

Aquatic invertebrate data were collected across eight sampling seasons, from 2009 to 2011, during the summer and winter high-flow periods and the fall low-flow period (Figure 6.2a). Mean discharge in 2010 was significantly higher than the other two years; the lowest mean discharge was observed in 2009. We collected invertebrate community samples from 20 sites representing perennial, intermittent, and ephemeral streams (Figure 6.1). In each sampling season, a subset of all 20 sites, which had flowing water, were visited and sampled. Each site consisted of a 100-m-long stream reach in which all available microhabitat (primarily riffles and pools) were sampled with a D-net (500-µm mesh). In riffle sites, 0.33 m^2 of stream substrate to a

depth of 5 cm was disturbed, and invertebrate samples were collected immediately downstream. In pools, the entire pool area was swept with a D-net at an effort of 10 s m^{-2} pool habitat. The samples were preserved in 95% ethanol and were identified in the laboratory to the finest taxonomic level possible, usually to genus or species for insects and family or order for non-insects (Schriever et al. 2015).

Legend

Annual Precipitation
unit: mm

▮	0
▮	0 - 344
▮	344 - 361
▮	361 - 381
▮	381 - 404
▮	404 - 434
▮	434 - 473
▮	473 - 526
▮	526 - 620
▮	620 - 771

★ USGS gauges
● Sensors
▲ Sampling Sites

Streams

— ephemeral
— intermittent
— perennial
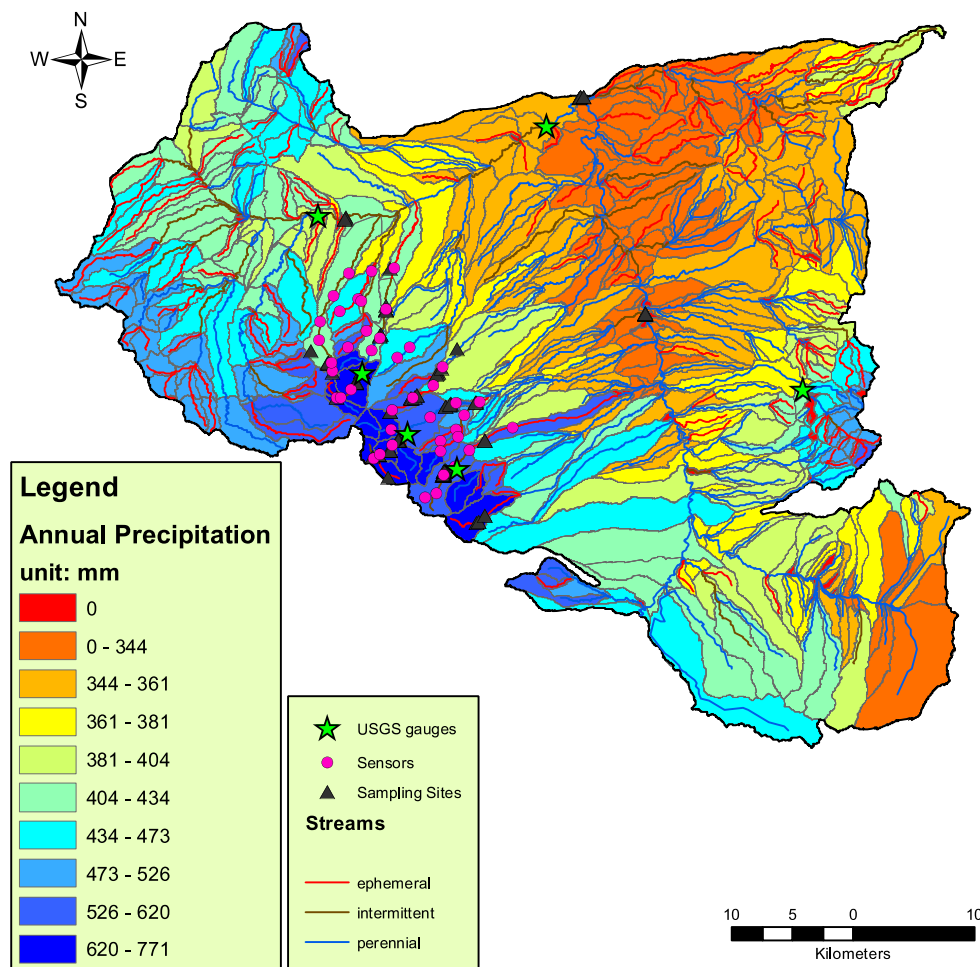
Figure 6.1. Huachuca Mountains (left) and San Pedro watershed (right), including streams labeled according to hydrologic classifications of perennial, intermittent, and ephemeral streams, annual precipitation, invertebrate sampling points, USGS flow gauges (from north to south on the map: STAID 09471400, 09471380, 09471310, 09470800, 09470750, and 09470700), and electrical resistant sensors for recording water permanence.

River network characteristics and stream types. We used data from the NHDPlus Version 2 to delineate the boundary of the San Pedro watershed and identify a total of 561 stream reaches

(Figure 6.1). High elevation streams are often fed by springs and demonstrate perennial flow regimes. Downstream of them, streams cross alluvial fans where surface water losses to evaporation and infiltration are high, and streams become intermittent. Surface flow in these intermittent streams persists for weeks to months after precipitation. Further downstream, the water table seldom rises above the streambed and surface flow occurs for very brief periods (< 1 day) in response to extreme precipitation events. These are ephemeral streams. Below the alluvial fans, perennial rivers flow through fluvial floodplains. To identify the hydrological type for each stream reach in the river network, i.e., ephemeral, intermittent, and perennial streams, we constructed a classification tree model using field sensor data on water permanence from Jaeger and Olden (2012).

Quantifying inter- and intra- annual hydrological variability. Discharge data during the study period (2009-2011) was used to determine the duration of high flow and low flow periods in a year. There are six USGS gauges located within the study area. Based on the discharge regime from these gauges between 2009 and 2011, we estimated 16 weeks for the duration of the winter high flow period, 12 weeks for the summer high flow period, and 12 weeks each for spring and fall low flow periods for an average year.

We obtained the spatial gradient of annual precipitation across the watershed from USGS National Atlas GIS data. This represented the precipitation spatial gradient in an average year. We extracted the precipitation for each catchment within the watershed. To simulate the inter-annual variability in precipitation, we obtained annual precipitation data (non-spatial) between 1922 and 2014 from NCEP North American Regional Reanalysis (NARR) by National Oceanic & Atmospheric Administration (NOAA) for southern Arizona. We used a first-order autoregressive model to fit this long-term dataset:

$$PT_t - \overline{PT} = \rho(PT_{t-1} - \overline{PT}) + Z_t \qquad (1)$$

where *PT* was annual precipitation, ρ was the lag-1 autocorrelation coefficient, and *Z* was the stochastic term. We fitted *Z* with different distributions, and found that a gamma distribution with shape parameter $k = 3.40$, scale parameter $\theta = 4.95$, and a shift of -16.86 (to keep $E[Z_t] = 0$), was the best fit.

Estimating habitat capacity. An important prerequisite for an effective neutral metacommunity model is reasonable estimation of habitat capacity (Muneepeerakul et al. 2008; Dong et al. 2015). Here, we assumed that water availability is a proxy of habitat capacity (*HC*), which is the amount of space and resources available to support species occupancy at any particular site. We made use of the power-law relationship between α diversity (watershed scale) and *HC*, which is conceptually similar to the well-known species-area relationship (species richness increases with sample area; here we replaced sample area with *HC*). We used the product of precipitation and watershed area (*PT×WA*) to estimate *HC*. We observed that α diversity first increased with *PT×WA*, peaked at an intermediate value, and decreased at high values of *PT×WA* (Online

Resource C). Based on this pattern from the observed data, we estimated habitat capacity of each catchment (HC_i) by its $PT \times WA$ via the following formula:

$$HC_i = \left(C(PT_i \times WT_i)^{0.9} exp(-PT_i \times WA_i / 4700) \right)^a \qquad (2)$$

where a and C parameters were to be determined by model fit.

Description of neutral metacommunity models. Four neutral metacommunity model variants were constructed with different patterns of temporal variability: (1) Basic Model—without any temporal variability; (2) Seasonal Model—including seasonality (intra-annual); (3) Annual Model—including inter-annual variability; and (4) Full Model—including both seasonality and inter-annual variability. All four model variants were implemented in the river network structure.

Basic Model. The Basic Model was similar to a model developed by Muneepeerakul et al. (2008), which included stochastic dispersal, reproduction, mortality, and speciation (Online Resource D). The dispersal kernel was assumed to be the bivariate Students' t or "2Dt" kernel (Clark et al. 1999), which can be written as

$$K_{ij} = C_j \frac{p}{\pi l_0^2 [1 + \left(\frac{L_{ij}}{l_0} \right)^2]^{p+1}} \qquad (3)$$

where K_{ij} is the probability that an organism produced at site j arrives at site i after dispersal; C_j is a normalization constant to ensure that for every site j, $\sum_i K_{ij} = 1$, i.e., no organisms traveled out of the metacommunity. L_{ij} is the Euclidean distance between two habitats (our preliminary results on distance decay relationship as shown in Online Resource E suggested that Euclidean distance is appropriate) . This dispersal kernel was determined by two parameters, l_0 and p. The 2Dt kernels were chosen because they can exhibit a wide range of behaviors, from the heavy-tailed Cauchy kernel when p approaches 0 to the thin-tailed Gaussian kernel when p approaches ∞ and others in between.

Seasonal Model. The Seasonal Model was modified from the Basic Model by incorporating varying habitat capacity and duration for each flow season. Perennial streams were assumed to have the same habitat capacity in all four seasons, equal to the value estimated by $PT \times WA$. The habitat capacity for intermittent and ephemeral streams varied with seasons, modified by a season-specific weight (< 1). The values of the weights were estimated from the observed species abundance data for corresponding stream types.

When the habitat capacity increases from one flow period to the next, there will be sites available to be occupied in that catchment. These unoccupied sites will be recolonized with a probability r. The recolonizing species can be a species already existing in the metacommunity with probability 1-v, or a new species with probability v. On the other hand, if the habitat capacity decreases from one flow period to the next, a randomly selected set of individuals dies, with the

number dying equal to the difference in habitat capacity between two flow periods. All other processes in the Seasonal Model were the same as in the Basic Model.

Annual Model. The Annual Model was developed from the Basic Model by incorporating inter-annual variability in habitat capacity introduced by inter-annual variability in precipitation, which was simulated using the first-order autoregressive model (see Section "Quantifying inter- and intra- annual hydrological variability"). From one year to the next, when mean precipitation changes, it proportionally changes the habitat capacity of each catchment and the duration of the high flow periods for each flow season within a year. However, for the Annual Model, the habitat capacity for each catchment did not change within a year. HC_i was therefore calculated as the mean HC_i across four flow periods weighted by the duration of each period. This guaranteed the same long-term average habitat capacity across models. As with the Seasonal Model, if habitat capacity increases, unoccupied sites appear in the first time step of a year and are recolonized with a probability r in the following time steps. The recolonizing species can be a species already existing in the metacommunity with probability $1-v$, or a new species, with probability v. If habitat capacity decreases from one year to the next, a randomly selected set of individuals die, the number dying equaling the difference in habitat capacity between two years.

Full Model. The Full Model simulated both seasonality and inter-annual hydrological variability. The annual precipitation changes with year, which proportionally changes the habitat capacity of each catchment. The duration of each flow period varied every year, i.e., the increase or decrease in the duration of the high flow periods was proportional to the increase or decrease of the precipitation in that year compared to precipitation in an average year.

Each time step in the model represented one week, and it took about 80,000 time steps (about 1500 y in model time) to reach a statistical steady state, i.e., when the biodiversity patterns became stabilized, and showed no directional trend in the mean local species richness or the total species richness. After the model reached steady state, we ran another 1000 y of model time to calculate average patterns.

Quantifying model goodness-of-fit. We used patterns of α and β diversity (measured by Chao similarity index; Chao et al. 2005) to assess the fit between observed and modeled results from the Full Model. The best-fit parameter set was chosen by the following procedure. We ran a number of simulations with different sets of parameters distributed over a wide range. For every simulation, we computed the error between data and model for the two biodiversity patterns: α and β diversity. The error for pattern k, E_k ($k = 1$ for α diversity, 2 for β diversity), was estimated by the mean square deviation between data and predicated values normalized by the data variance; this can be expressed as follows:

$$E_k = \frac{\sum_{i=1}^{N_k} (x_{k,i} - \hat{x}_{k,i})^2}{\sum_{i=1}^{N_k} (x_{k,i} - \langle x_k \rangle)^2} \tag{4}$$

where N_k was the number of data points used in fitting pattern k, $x_{k,i}$ and $\hat{x}_{k,i}$ were data point i (data points from all eight sampling events across three years) of pattern k and its predicted value, respectively, and $\langle x_k \rangle$ the mean value of the data points of pattern k. (E_k is basically one minus the Nash-Sutcliffe coefficient, a commonly used metric for performance of hydrological models.) We then defined the total error, *TE*, of each parameter set as $E_1 + E_2$. *TE* was used as a metric to compare model goodness-of-fit, and the parameter set with minimum *TE* was selected as the best model.

The best-fit parameters for the Full Model were applied to the other three model variants (Basic, Seasonal, and Annual Models) so that there was only one set of underlying processes across all these variants. For each of the other three model variants, we assessed the model goodness-of-fit with the observed data at corresponding aggregate levels. In addition to hydrological fluctuation, we explored the effect of two other factors, species dispersal mechanisms and the spatial extent of the sampling sites, on the relative importance of neutral processes.

6.4   Results

Analysis of the empirical dataset (prior to modeling) showed that local species richness (α diversity) was consistently higher in perennial streams than that in non-perennial streams across all sampling seasons. The model performance varied widely across the model variants (Table 6.1, Table 6.2). Including temporal variability (seasonality and/or inter-annual variability) resulted in some improvements in model performance (Table 6.1). The Full Model that explicitly incorporated both seasonal and inter-annual variability provided the best model fit. Model performance was slightly better when including only inter-annual variability, compared to including only seasonality, indicating that inter-annual variability likely played a more important role than seasonality in shaping species abundance and distribution. The Basic Model, which did not incorporate any temporal variability, demonstrated the poorest performance among all model variants. These results support the importance of including temporal variability in the neutral models.

Aggregated by year, the wettest year (2011) had the best fit for α diversity (Table 6.1). Aggregated by season, model performance for the fall season exceeded that for the summer or winter season for α and β diversity patterns. We then checked the year- and season- specific result from the Full Model (Table 6.2). For α diversity, the best fit occurred in 2010 summer, the high flow period in a very wet year, and the poorest fit occurred in 2009 summer and 2011 fall. Model performance for β diversity was strongest for 2010 summer and 2011 winter and weakest for fall 2011. Because of the high inter- and intra-annual variability in hydrology, we used the mean stream discharge during the sampling period to quantify the "wetness" of each period in different seasons and years: the average of instantaneous discharge from all the USGS gauges within the system during the sampling month. We found that the model performance was poorest for the intermediate range of discharge (Figure 6.2b). When the mean discharge of the sampling month was below $0.05 \text{ m}^3 \text{s}^{-1}$, the model's ability to predict the α and β patterns decreased with

the discharge, i.e., better fit in periods with lower discharges. However, when the mean discharge exceeded about 0.25 $m^3 s^{-1}$ in the summer of 2010, a relatively good model fit was obtained.

Using the aggregated result from the Full Model, we also compared the model goodness-of-fit for two different stream types, i.e., perennial and non-perennial streams. Model performance was notably better in predicting biodiversity patterns for perennial streams than it did for non-perennial streams (Table 6.3). Our findings on changes of model performances in different times and across stream types are robust to changes in parameter values (Figure 6.3). For both α and β diversity, the absolute model goodness-of-fit could be improved or worsened depending on the values of parameters, but relative differences in model goodness-of-fit did not change.

For the other factors that might influence model performance, we found there was no significant correlation between the proportion of aerial dispersal species in the metacommunity and the model goodness-of-fit. The model performance forβdiversity notably improved when the sampling sites (which varied across seasons) were more spatially dispersed.

Table 6.1 Model performance (measured by total error) for the four models with different complexity for temporal variability. For the cases of seasonality only, annual only, and no temporal variability, observed data were compared against results from two models. For example, for "Seasonality only", the observed data were compared with the predictions from the seasonal model, and from the full model; we aggregated season- and year-specific results from full model to obtain the average result for each season (across three years).

	Seasonality & Annual	Seasonality only		Annual only		No temporal variability	
	Full Model	Full Model (aggregated)	Seasonal Model	Full Model (aggregated)	Annual Model	Full Model (aggregated)	Basic Model
α diversity	0.64	0.73	1.01	0.68	0.84	1.00	1.48
		*sm =1.07	sm = 1.49	§$y09$ = 0.67	$y09$ = 0.73		
		†wt =0.86	wt = 0.94	‖$y10$ = 0.59	$y10$ = 1.41		
		‡fl =0.64	fl = 0.61	¶$y11$ = 0.57	$y11$ = 0.61		
β diversity	0.84	0.93	0.98	0.90;	0.95	1.01	1.07
		sm = 1.05	sm = 1.08	$y09$ = 0.80	$y09$ = 0.97		
		wt = 0.98	wt = 1.02	$y10$ = 1.00	$y10$ = 1.00		
		fl = 0.80	fl = 0.86	$y11$ = 0.80	$y11$ = 0.80		

*summer; †winter; ‡fall; §year 2009; ‖year 2010; ¶year 2011

Table 6.2 Performance of the Full Model (measured by total error) for prediction of α diversity and β diversity (Chao similarity index) across the eight sampling seasons.

Metrics	Summer			Fall			Winter	
	2009	2010	2011	2009	2010	2011	2010	2011
α diversity	1.98	0.51	0.56	0.54	0.53	2.28	1.12	0.70
β diversity	1.19	0.64	0.92	0.58	0.79	2.80	1.00	0.44

Table 6.3 Model performance for Full Model (measured by total error) for perennial and non-perennial streams.

Stream type	α diversity	β diversity
Perennial	0.68	0.78
Non-perennial	1.21	1.36

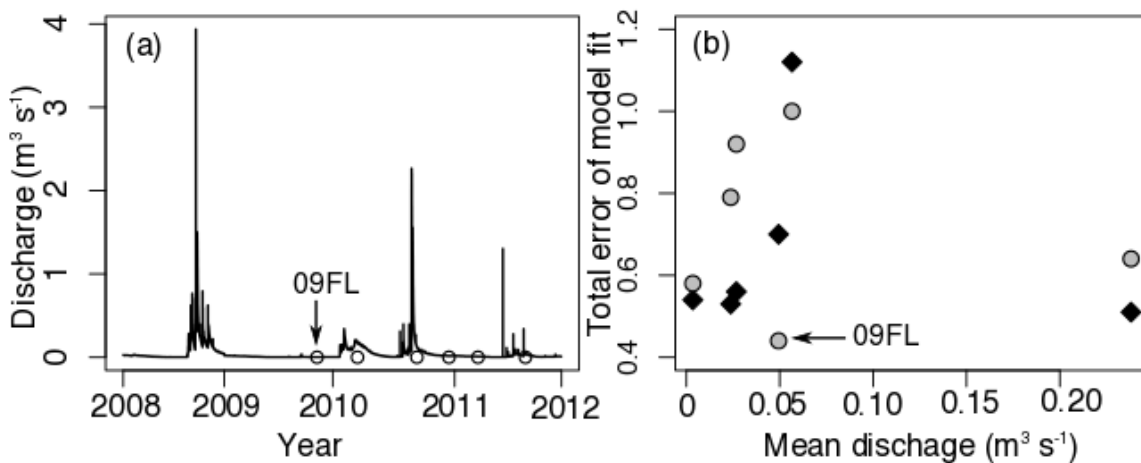Figure 6.2 The effect of hydrology on the model performance. (a) Instantaneous discharge from one of the gauges (#09470800; Fig. 1) in the system between 2008 and 2011. Different gauges had different absolute discharge values, but showed similar hydrological patterns; the round circle indicated the time when sampling occurred; and (b) relationship of model fits for those seasons in which a reasonable fit was

obtained, *vs.* average discharge of across the gauges within the system during the sampling month. The point 2009 Fall had much lower total error for β diversity – greater importance of neutral processes, likely a result of prolonged drying phase (a), not captured by discharge.
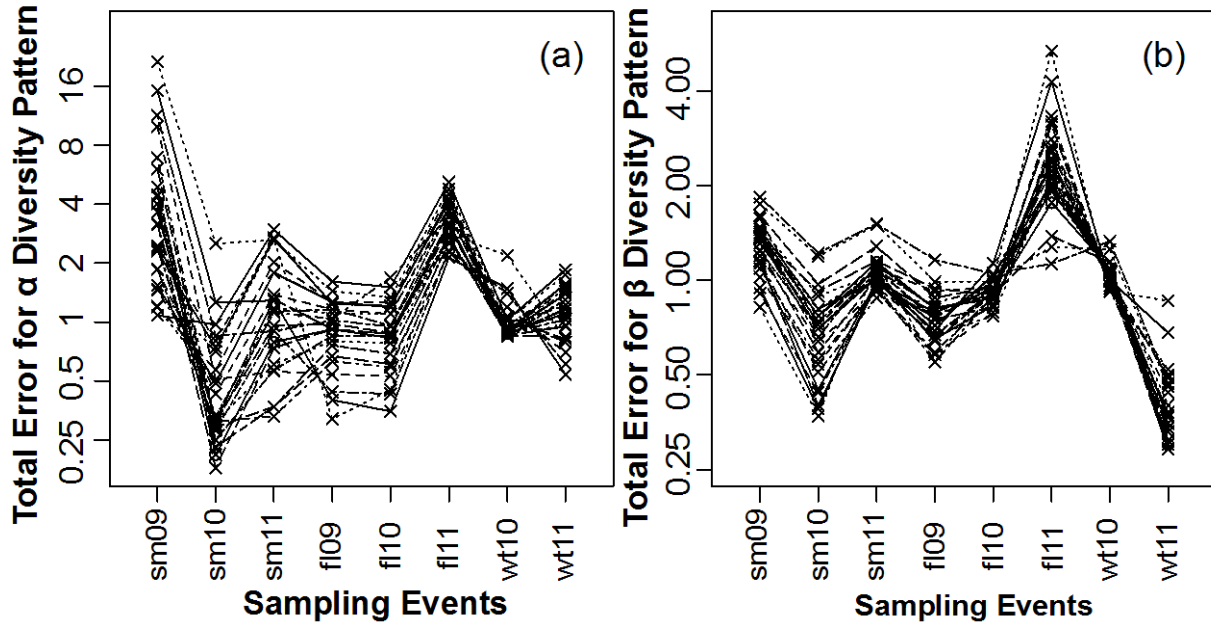
Figure 6.3 The total error of the Full Model fitted with different parameter sets (*n* = 28, results from the same parameter set were connected with a line) within a reasonable range of values for (a) α diversity pattern, and (b) β diversity pattern across 8 sampling events in three years (2009, 2010, 2011). Season abbreviations are as follows, summer ('sm'), fall ('fl'), winter ('wt').

6.5   Discussion

In this paper, we developed spatially and temporally explicit neutral models for aquatic invertebrate communities in dryland streams to investigate how the relative importance of neutral processes vary in space and in time. Despite some non-ideal conditions for neutrality (Gravel et al. 2006)—relatively low richness compared to streams in other biomes (Vinson and Hawkins 2003) and generally strong dispersal limitation among freshwater invertebrates (Bohonak and Jenkins 2003)—aquatic invertebrate communities in dryland streams offer great natural laboratories for investigating the effects of temporal variability on the relative strength of niche vs. neutral processes in community assembly. These streams are highly variable in time and strongly heterogeneous in space and harbor ecological communities that have constantly experienced such environmental variability. We used the goodness of fit of neutral metacommunity models to evaluate the relative importance of neutral processes in perennial and non-perennial streams and under different hydrological conditions. We found stronger effect of neutral processes in perennial streams and during very low and very high flow periods. These

results suggested the changes of assembly processes both in space and time for the aquatic invertebrate community in this dryland stream network.

The neutral models provided consistently better model fits for invertebrate communities of perennial streams than for non-perennial streams (Table 6.3). While both perennial and non-perennial streams experience disturbances in the form of floods, droughts in non-perennial streams are likely stronger disturbances for aquatic macroinvertebrates. Leigh and Datry (2016) recently assessed the influence of drying on macroinvertebrate communities in Australia and Europe over broad spatial and temporal scales, and found that drying is more important to species diversity compared to other flow-related determinants. Fritz and Dodds (2004) showed that resistance and resilience of stream macroinvertebrates were typically greater to floods than to drying. In our own study system in Arizona, Bogan and Lytle (2011) monitored two stream pools for eight years, and found that invertebrate communities underwent a regime shift in species composition in response to a transition from perennial flow to intermittent. In this sense, perennial streams, despite their frequent flood disturbances, are relatively less harsh habitats for macroinvertebrate communities. This agrees with the theoretical prediction that neutral processes are more important in systems that have less environmental fluctuations (Chase 2007): flow intermittency serves as a stronger environmental filter to select for species with biological traits and behavioral strategies to survive drying phases, leading to greater effect of niche processes in non-perennial streams and relatively stronger neutral processes in perennial ones.

Averaging the entire dryland stream network, the model goodness of fit was greatest in very high-flow and very low-flow periods and lowest in the intermediate flow period, a result that holds regardless of model parameters (Figure 6.3). The low and high ends of flow conditions represent disturbances at their greatest severity—droughts on the one end and floods on the other. The flood in the summer of 2010 had a 5-year flood, and the sampling took place within two weeks after that flood. In contrast, before the fall sampling campaign of 2009 (November 2009), the system had been in drying phase for more than a year without any flood. The system usually receives half precipitation during summer monsoon and another half during winter, but the precipitation is highly variable from year to year – after 2008 summer monsoon until the end of 2009, for a consecutive ~15months, there was barely any rainfall input to the system. At these two extremes of flow conditions, we found greater importance of neutral processes. This might be because extremely severe disturbances cause random extinction and recolonization even among the core of the regional taxa that are most resistant to disturbance (Lepori and Malmqvist 2009). Faced with very large floods, the protection against dislodgement to resist floods provided by biological traits of the invertebrate species, such as small body size, streamlined body-shape, and ability for attachment to the substratum (Poff and Ward 1989) is probably very limited. Similarly, faced with severe and prolonged drought, water-retaining refuges, which are essential for the maintenance of most populations, contract in size and water quality conditions worsen in time (Boulton and Lake 1992). These results suggest that when disturbances are sufficiently severe, be they droughts or floods, the mortality rate may decouple from the species' traits and

identity, resulting in more neutral process-dominated biodiversity patterns. Lepori and Malmqvist (2009) showed similar results where severe disturbance triggers neutral processes for aquatic invertebrate community in streams in North Sweden. All in all, these findings suggest that the theoretical framework be modified to recognize that the net effect of disturbance on both niche and neutral processes is non-monotonic and severity-dependent.

The promoting effect of severe disturbance on neutral processes was likely smoothed out when we compared perennial and non-perennial streams: we took average of eight different hydrological conditions, most of which represented intermediate disturbance conditions. Hence, perennial streams still showed stronger neutral processes than non-perennial ones. There are also alternative explanations for greater importance of neutral processes during very high flow and very low flow periods. For example, when stream flow is very low or very high, the whole landscape is more homogeneous (uniformly low (or zero) or high stream flow), while intermediate flow promotes higher flow heterogeneity across landscapes by creating high degrees of habitat patchiness. Theoretical models (Gravel et al. 2006; Scheffer and van Nes 2006) suggest that the validity of the neutrality assumptions increases as more homogeneous environment enables high niche overlap. This explanation is somewhat speculative at this point, as one needs quantification of landscape heterogeneity to support it—a worthwhile future research direction.

Finally, we want to stress the importance of model formulation. Our results showed that model performance improved substantially when seasonality and inter-annual variability were incorporated into the neutral metacommunity models. This suggests that model formulation—not necessarily the validity of the neutrality assumption alone—is an important determinant of neutral model performance (Rosindell et al. 2011). Other more complex hydrological effects such as legacy effect of hydrological disturbance (Parsons et al. 2005) and cross-scale interactions (Peters et al. 2004; Sivapalan and Blöschl 2015) can also play a role in influencing habitat capacity. Etienne (2007) urged modelers to incorporate spatial structure into their efforts; similarly we suggest that incorporating temporal variability is a necessary, albeit challenging, component to include in biodiversity models.

6.6   Acknowledgements

7   Dispersal strength determines meta-communities in a dendritic riverine network

Synopsis: The model structures introduced in the previous sections provide a general platform for examining biodiversity from both a niche and a neutral perspective. The following section explores the roles of dispersal ability, site hydroperiod, and among-site distance as factors that can explain when niche vs. neutral factors might influence community structure.

7.1   Introduction

Studying patterns of biological diversity has been the foundation of numerous ecological pursuits over the past two centuries. Distance decay relationships (DDRs) – which describe the biogeographical phenomenon where taxonomic similarity between localities decreases or decays as the distance between them increases – have received considerable interest among ecologists (Nekola & White, 1999). Indeed, this ecological pattern is encapsulated in Tobler's first law of geography, which states that 'everything is related to everything else, but near things are more related than distant things' (Tobler, 1970, p. 236). DDRs have now been studied across a wide range of organisms and environments (reviewed in Soininen *et al.*, 2007), but are still relatively understudied in riverine ecosystems (Thompson & Townsend, 2006; Leprieur *et al.*, 2009; Brown & Swan, 2010; Bonada *et al.*, 2012; Warfe *et al.*, 2013). This is largely because streams and rivers are organized as complex dendritic networks rather than simple linear systems (Benda *et al.*, 2004; Campbell Grant *et al.*, 2007; Erős *et al.*, 2012), thus necessitating the incorporation of network connectivity to explore the interactions among communities that are linked by dispersal (Fausch *et al.*, 2002).

The environmental phenomena that drive any particular DDR can be decomposed into local and regional factors. Local factors include site-specific environmental attributes (e.g. substrate composition, channel depth, water temperature and chemistry) and biotic interactions (e.g., predator, competition, parasitism) that serve as filters, excluding some taxa and favouring others (Poff, 1997; Townsend *et al.*, 1997). Regional factors include landscape-level features that facilitate or impede the movement of organisms across landscapes. These features may include the dendritic structure of stream networks (Fausch *et al.*, 2002; Benda *et al.*, 2004), the spatial arrangement of suitable habitat patches across the landscape (Campbell Grant *et al.*, 2007; Erős *et al.*, 2012; Phillipsen & Lytle, 2013), and the simple Euclidean distance between sites. Therefore, a full understanding of the ecological processes underlying DDR patterns in stream networks must account at least for three main factors: environmental filters, dispersal of organisms and network topology.

Environmental harshness, both in terms of hydrologic regimes and physical conditions, can influence the role of local and regional forces shaping biodiversity patterns (Brown *et al.*, 2011;

Heino, 2011). For example, unstable environments (e.g. aquatic habitats that experience severe, recurrent droughts) show a high degree of niche filtering, allowing only those species adapted to the local conditions to persist (Poff, 1997; Chase, 2007). In these circumstances, environmental forcing plays a much greater role than biotic interactions, such as predation or competition, in shaping patterns of species occurrence and community composition (Jackson et al. 2001). Therefore, harsh environmental conditions may cause meta-communities to be structured by local factors (Urban, 2004) and DDRs may not meet the expectation of decreasing community similarity with increasing distance.

Dispersal of aquatic-obligate riverine organisms is highly constrained by flow connectivity (Fausch *et al.*, 2002; Hughes, 2007; Schick & Lindley, 2007). In contrast, aquatic organisms that can disperse overland, such as flying forms of adult aquatic insects, can move both along drainages and across drainage divides (Bilton *et al.*, 2001; Petersen *et al.*, 2004). Therefore, variability in dispersal mode and ability will determine the extent to which local and regional factors structure assemblages of organisms (Bohonak & Jenkins, 2003; Cottenie & De Meester, 2004) and may be reflected in the shape of the DDR. For example, studies on aquatic invertebrate meta-communities in stream networks have reported that increasing dispersal strength results in a weakening of DDRs due to relaxation of dispersal limitation (Thompson & Townsend, 2006; Brown *et al.*, 2011). Very high dispersal rates could cause the homogenization of communities, because organisms can disperse to all available habitats and only the strongest competitors will survive (Kneitel & Miller, 2003; Leibold *et al.*, 2004).

The network topology, or spatial structure of the river network, also has important implications for dispersal and resulting meta-community structure (Muneepeerakul *et al.*, 2008; Auerbach & Poff, 2011). The use of within-network and overland dispersal pathways by aquatic organisms largely depends on the connectivity between the habitat branches, with the loss of connectivity constraining within-network dispersal (Fagan, 2002). Although critical for understanding the potential mechanisms shaping DDRs (Brown *et al.*, 2011), landscape resistance to the dispersal of organisms has been largely neglected in meta-community analyses (Moritz *et al.*, 2013). Landscape resistance quantifies 'distances' between communities that may yield more biologically informative DDRs than straight-line Euclidean distance, such as those associated with barriers to dispersal (e.g. high mountains or cliffs). To the present date, only Euclidean and network distance (i.e. the distance between sites along the riverine dendritic network) have been applied to stream networks, which fails to consider more realistic landscape variables in DDR analyses (McRae *et al.*, 2008).

In this study, we present a novel application of a landscape resistance modelling approach, originally developed for landscape genetic studies, to understand local and regional drivers of community structure. Dryland streams were used as a model system to test how environmental stability, dispersal capacity, and network topology interact to structure aquatic meta-communities in dendritic networks. These streams experience frequent droughts and floods, which lead to strong niche filtering of stream organisms (Lytle, 2002; Lytle & Poff, 2004), with perennial

habitats serving as refugia for species that need water during their entire life cycle to survive (Bogan & Lytle, 2011; Phillipsen & Lytle, 2013). Therefore, the high temporal and spatial variation in environmental conditions may disrupt expected longitudinal patterns of species' replacement along the network (Bogan *et al.*, 2013). In these systems DDRs are expected to be weak or non-existent, with adjacent sites showing very different aquatic assemblages as a result of large among-site variation in environmental conditions (e.g. one site may flow year-round, while an adjacent site may flow only during rainy seasons). We focused on aquatic invertebrates because they possess a wide range of dispersal capacities (Bilton *et al.*, 2001; Bohonak & Jenkins, 2003) and are present over a wide range of environmental conditions (Rosenberg & Resh, 1993; Merritt *et al.*, 2008), as exemplified by the great diversity of biological traits that they exhibit (Statzner *et al.*, 2004; Poff *et al.*, 2006).

The aim of our study was to use DDRs to investigate the relationship between local and regional factors in explaining aquatic meta-community structure in fragmented dendritic networks. Here we define fragmentation as the loss of surface water connectivity along the river network. During low precipitation periods (typically in late spring and summer) some dryland streams experience very low flow, with sections becoming disconnected pools separated from one another by dry stream reaches. We used fine-scale local environmental variables and landscape resistance metrics to quantify the influence of local and regional drivers on DDRs for groups of species with different dispersal capacities. The following hypotheses were tested:

H_1: DDRs should be weak for very strong and very weak dispersers (at the ends of the dispersal gradient) because meta-communities of weak dispersers show little spatial structure and meta-communities of strong dispersers are homogenized by competition. We predicted that DDR would be strongest in species with moderate dispersal strength.

H_2: Owing to high network fragmentation in dryland streams (i.e. longitudinal flow disruption during long dry seasons), no significant DDR should be found when using network distance. We predicted that network distance would have low explanatory power because of high spatial and temporal stream fragmentation, while our approach that considers landscape resistance to dispersal would provide greater explanatory power.

H_3: Owing to strong niche filtering (i.e. high environmental heterogeneity), DDRs associated with flow and environmental characteristics should be consistently stronger than DDRs associated with landscape resistance variables, regardless of the dispersal strength of the organisms. We predicted that DDRs associated with flow and environmental characteristics would be significant, regardless of species' dispersal abilities.

7.2   Materials and methods

We sampled aquatic invertebrates at 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA (Figure 7.1).

Streams in the area generally have perennial flow in montane headwaters, intermittent flow in upper alluvial fan reaches, ephemeral flow lower on alluvial fans, and then alternating perennial and intermittent reaches in valley rivers (Bogan *et al.*, 2013). We distributed our sample sites among perennial, intermittent and ephemeral reaches (classification follows Levick *et al*., 2008), but used a continuous flow metric to quantify permanence (see below). Sites were sampled three times a year (March/April, August/September, and November/December) between 2009 and 2011. The number of sites and samples collected differed among streams because not all sites had flow or all microhabitats during each sampling event. The study period spanned numerous dry seasons, several periods of ephemeral flows from summer monsoon rains, and one period of intermittent flows resulting from a wet winter. The majority of the sampling occurred during the fall (Nov/Dec) and winter (Mar/Apr) seasons for a total of 144 site $\times$ sampling event combinations.

Both riffle and pool microhabitats were sampled at each site, when present. For riffle samples we disturbed 0.33 m^2 of stream substrate to a depth of 5 cm while capturing invertebrates immediately downstream with a D-net (500-µm mesh). Pool samples consisted of sweeping the entire pool area including water column, surface, and pool benthos with a D-net at an effort of 10 s for every 1 m^2 of pool habitat (following Bogan & Lytle, 2007). Abundances from replicate microhabitat samples collected from the same site during the same sampling event (e.g. three riffles in November) were summed for each taxon and divided by the number of replicates to acquire relative abundances. Samples were preserved in 95% ethanol and invertebrates were identified in the laboratory to the finest taxonomic level practical, usually to genus or species for insects (including Chironomidae) and family or order for non-insects.
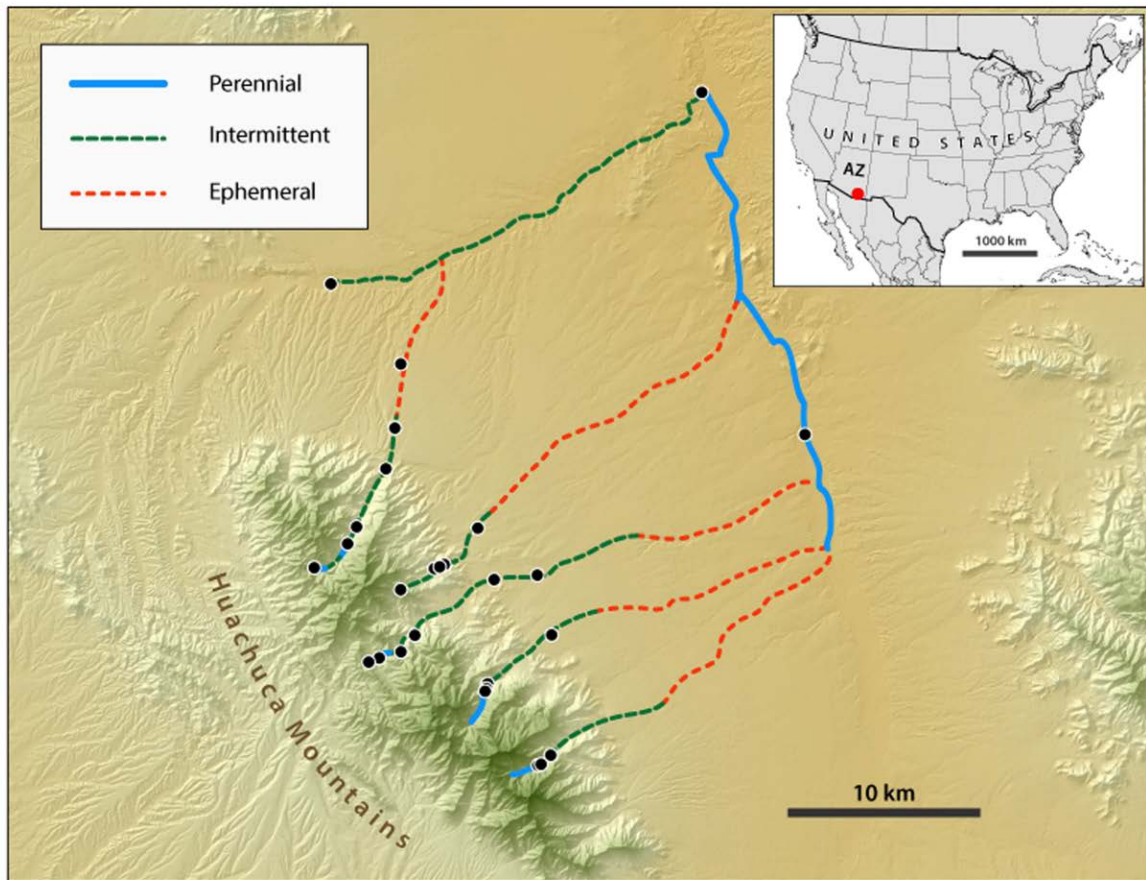
Figure 7.1. Map of sampling localities for stream invertebrates in south-eastern Arizona (USA). Inset map shows the location of the study area. Continuous blue line, perennial streams; short-dashed green line, intermittent streams; long-dashed red line, ephemeral streams. Black circles represent sampling localities. The map is based on a digital elevation model (DEM) at 10 m resolution.

During each visit, we measured water temperature, pH (Whatman pH indicators, Whatman International, Maidstone, UK) and conductivity (Milwaukee waterproof EC meter C65; Milwaukee Instruments, Rocky Mount, NC, USA), visually estimated canopy cover and benthic substrate on a percentage cover scale (0–100%; substrate categories: silt, sand, gravel, cobble and bedrock). We measured the timing and duration of streamflow through the deployment of 15 electrical resistance sensors (Jaeger & Olden, 2012), each representing the hydrological conditions at the nearest location of invertebrate sampling. The sensors logged the presence or absence of water in the stream channel at 15-min intervals from April 2010 to December 2011. From the sensor data, we calculated four hydrological metrics for each site: % flow permanence by year, mean % flow permanence by season (spring = May–June; monsoon = July–September; fall = October–November; winter = December–April), mean duration (number of days) of zero flow periods (ZFP) each year, and total number of ZFP each year. For the two flow permanence metrics and duration of ZFP, we summed 15-min time periods of both wet and dry conditions for the sampling period and for individual zero flow periods, converting the time unit to either days or years as appropriate for the final stream flow metric. We used an average of 2010 and 2011 flow data to estimate flow conditions for the November 2009 invertebrate sampling period (16 samples) that occurred prior to the deployment of sensors. Flow permanence is the percentage of time a given reach is wetted or flowing, while the duration of ZFP indicates how long (in days) a given reach is dry during each drying event. For example, a site with permanent stream flow would have a flow permanence of 100% and would receive a value of 0 for ZFP duration. While these metrics were all calculated from the flow sensor records, they were designed to characterize distinct components of the hydrological regime that may influence aquatic invertebrate occurrence and abundance.

7.3 Distance measures

We used four regional distance metrics (Table 7.1, Figure 7.2), two of which described to the physical distance between sites (geographical distance and network distance) and two of which described the resistance of the landscape to dispersal (topographic distance and perennial distance). *Geographical distance* is simply the straight-line Euclidean distance between two sites as determined from map coordinates. *Network distance* was generated via a least-cost path analysis in ArcGIS 9.3 (ESRI, Redlands, CA, USA). For this variable, only one pathway connects each pair of sites, and this pathway is restricted to the stream network. *Topographic distance* assumes that dispersal occurs along concave corridors such as streambeds, dry gullies, or low saddle points along mountain ridges. Flying and crawling insect adults are likely to follow these relatively cool and moist pathways to disperse from one wetted site to another (Bogan & Boersma, 2012; Phillipsen & Lytle, 2013). *Perennial distance* assumes that isolated perennial freshwater habitats act as stepping-stones for dispersal among communities in fragmented dendritic networks. For example, in arid landscapes perennial habitats are known to be critical for the survival of certain aquatic species when rivers cease to flow during droughts (Chester & Robson, 2011).

We generated the four regional distance measures from landscape data layers obtained from the Arizona State Land Department (https://land.az.gov/). Data layers used in our analyses included a digital elevation model (DEM; 10 m resolution), the stream network of the region (from the National Hydrology Dataset), and a map of perennial stream habitats. The latter was constructed using data for the San Pedro River watershed from the Nature Conservancy (http://www.azconservation.org/) combined with observations from field studies in the region (e.g. Bogan & Lytle, 2007; Bogan *et al*., 2013). We used ArcGIS 9.3 to generate new data layers and to calculate the distance (km) between all pairs of sites. The distances related to landscape resistance (topographic and perennial distances) were generated from the GIS data layers in the form of pixelated maps (i.e. rasters). Each raster map was used as input for the program Circuitscape (McRae, 2006). Circuitscape calculates the resistance of the landscape to dispersal between each pair of sites (analogous to electrical resistance in a circuit diagram), allowing for multiple pathways between sites. This pairwise resistance is a summation of the resistances of individual pixels in the input map. Pixels with high input values are hypothesized to offer high resistance to movement, and vice versa. Thus, pairwise resistances from Circuitscape model the structural connectivity of communities, based on the landscape/habitat feature represented by the input map. We used the original values of the map pixels to assign resistance values to the raster maps. Using the original pixel values is more conservative than assigning relative costs of landscape features based on expert opinion (a practice that some have questioned; Spear *et al*., 2010). Before running the Circuitscape analysis, we transformed the original values of the maps so that they were all on the same scale (1 for lowest resistance, 10 000 for highest resistance; results were qualitatively similar for different values of highest resistance). We performed a separate Circuitscape analysis for both topographic and perennial distances, generating their two independent data sets of all pairwise resistance distances as output. See Phillipsen & Lytle (2013) for an example of Circuitscape output in a population evolution context and how this relates to the underlying distance metrics.

In addition to the four regional distance measures, two local ecological distance measures were calculated: habitat distance and flow regime distance. *Habitat distance* was calculated as the dissimilarity between the multivariate centroids of each pair of sites based on their environmental characteristics, including canopy cover, conductivity, pH, and % of bedrock, cobble, gravel, sand and fines. *Flow regime distance* was calculated as the dissimilarity between the multivariate centroids of each pair of sites from a composite of flow metrics: % flow permanence in year of sample, % flow permanence by season, duration of zero flow periods each year (mean) and total number of zero flow periods each year. All variables were normalized (mean = 0; SD = 1) before analysis.
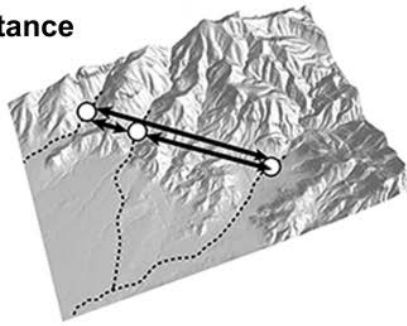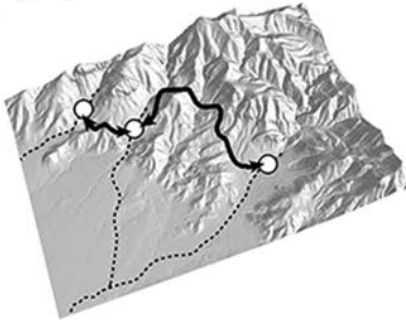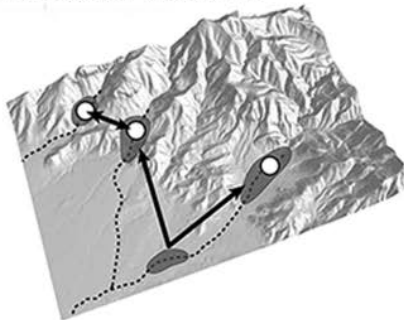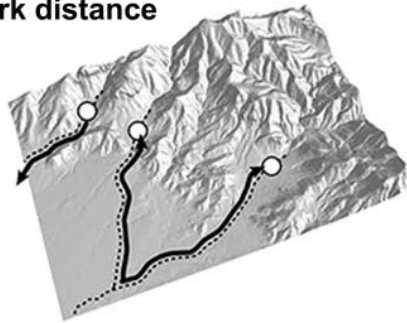
Figure 7.2 Hypothetical scenarios of species dispersal among sites in dryland streams based on each of the four regional distance metrics. In each scenario, the locations of three hypothetical communities are shown as white circles in a generic mountain landscape. Streams are depicted by dotted lines and thick black lines with arrowheads represent bi-directional species flow between pairs of communities. The paths of species dispersal in each scenario are determined by the hypothesized resistance to dispersal associated with the given landscape variable. In the topography scenario, for example, the underlying hypothesis is that dispersal is easiest in areas with strongly concave topography. Thus, gene flow is expected to be highest through areas with concave topography (shown as grey polygons in the figure). See Table 3.1 for more detail on each of the regional distance metrics.

Table 7.1 Details of the four regional distance metrics used in this study.

Distance metric	Explanation	Hypothesized relationship to species flow
Geographical distance	Straight-line distance between sites in two-dimensional space.	Dispersal increases when the geographical distance between a pair of sites decreases.
Topographic distance	Pairwise resistances between sites based on low resistance of map pixels with concave topography and high resistance of pixels with convex topography.	Dispersal is highest in areas with strongly concave topography. Dispersal is lowest across areas with strongly convex topography.
Perennial distance	Pairwise resistances between sites based on low resistance of map pixels in patches of perennial freshwater habitats and high resistance of pixels in the matrix between these patches.	Dispersal increases in the presence of perennial freshwater habitats.
Network distance (stream network)	Pairwise least-cost paths between sites that strictly follow the stream/river network. Only one path exists between any pair of sites.	Dispersal occurs only within the stream/river network.

7.4   Statistical analyses

Prior to analyses, we placed each of the 225 aquatic invertebrate taxa into one of four categories: weak, local, moderate and strong dispersers (see Appendix A). Weak dispersers (17 taxa) are aquatic obligates that spend nearly all of their life cycle within the stream (e.g. *Abedus herberti*). Local dispersers (142 taxa) have flying adult stages but can only travel short distances owing to their short life cycles and/or weak flying musculature (e.g. *Hydrobaenus* sp.). Moderate

dispersers (64 taxa) have flying adult stages that can travel long distances but cannot cover the entire geographical range of our study (e.g. *Enochrus aridus*). Strong dispersers (10 taxa) are powerful fliers that can travel between any of the sites in our studied geographical range (e.g. *Lethocerus medius*). These categories were derived from a trait database specific to the study region built from over 80 publications from primary literature, existing databases and expert judgment (Schriever *et al.*, in press). Abundance data were log (x+1) transformed and then used to calculate the Chao dissimilarity index among all pairs of sites (using the function 'vegdist' in the R package vegan; Oksanen *et al.*, 2013). The Chao index was the most appropriate dissimilarity index to use because each dispersal ability group had a different number of taxa; it is intended to account for the effect of unseen shared species and thus reduce sample-size bias (Chao *et al.*, 2005). Habitat distance, flow regime distance and the four landscape distances (Table 3.1) were used as independent explanatory variables of Chao's index for each group of species (weak, local, moderate and strong dispersers). Spearman correlation tests were performed between all pairs of the explanatory variables. For those variables showing strong correlation (i.e. Spearman's $\rho > 0.5$ and *P*-value < 0.01), we used partial Mantel tests (mantel function in vegan package) to compare community data to the explanatory variable of interest while controlling for the correlated variable (Legendre & Legendre, 2012). The differences in the relationship between community dissimilarity and each of the distance metrics (geographical, network, topographic, perennial, flow regime and habitat distances) across dispersal classes was tested through an analysis of covariance (ANCOVA; Legendre & Legendre, 2012) with Chao dissimilarity as the dependent variable, each driver as a covariate, and the dispersal class as the grouping factor.

We fitted linear models to each distance metric, and performed *F*-tests to assess model performance. Models were tested for linearity using the diagnostic plots for generalized linear models. We used the glm.diag.plots function in the R package BOOT (Davison & Hinkley, 1997; Canty & Ripley, 2014), which makes a plot of jackknife deviance residuals against linear predictor, normal scores plots of standardized deviance residuals, plot of approximate Cook statistics against leverage/(1 − leverage), and case plot of Cook statistic. After validating the models we used an information-theoretic approach to compare the contribution of different explanatory variables that best described differences in invertebrate community composition. We derived the log-likelihood for each model and calculated Akaike's information criterion (AIC; Akaike, 1973; Burnham & Anderson, 2002) to rank the models from lowest to highest AIC. We only compared single variable models and the combination of local environmental distance metrics (flow regime and habitat) and landscape distance metrics (geographical, topographic, perennial and network distances), because our aim was to compare the importance of local versus regional filters for aquatic invertebrate meta-communities across a gradient of dispersal strength. Once the models were ranked, additional information-theoretic metrics were calculated. The difference between the AIC of a particular model and the AIC of the estimated best-fitting model (i.e. the model with the lowest AIC) is ∆AIC. We also calculated Akaike weights, the probability that the model is actually the best-fitting of the candidate models. The sum of Akaike

weights across the models is 1.0. When the weight of the model with the lowest AIC is not close to 1.0, there is evidence for model selection uncertainty. We accounted for the non-independence of our data (represented by pairwise distances among sites) by using an R^2 approach for fixed effects in a linear mixed model to adjust for the inflation of sample size (Edwards *et al.*, 2008). As both the AIC and mixed model approaches yielded similar results, we only report the adjusted R^2 values for fixed effects (Table 7.2). The selection of AIC over adjusted R^2 values was based on the limited use of adjusted R^2 values in model building, owing to the lack of diagnostic and selection tools for linear mixed models (Edwards *et al.*, 2008). All analyses were conducted in R version 3.0.2 (R Core Team, 2013) and significance was assigned at $P < 0.05$. Bonferroni correction was used to adjust *P*-values for multiple comparisons.

7.5   Results

The six distance metrics displayed weak pairwise correlations. Only geographical, topographic and perennial distances were significantly correlated (Figure 7.3). Habitat and flow regime distances significantly explained community dissimilarity, regardless of the species' dispersal abilities (Table 7.2). Geographical, topographic and perennial distances significantly explained community dissimilarity for all dispersal groups except for the weak dispersers, and had a higher explanatory power for strong dispersers. Network distance was not a significant predictor for any dispersal group. Associations between community dissimilarity and the explanatory variables varied considerably among the four dispersal groups (Figure 7.4). The relationship between community dissimilarity and the six distance metrics differed across the dispersal categories for all but one metric (network distance; Table 7.3).

Partial Mantel tests revealed that: (1) geographical distance was significantly correlated with the composition of strong dispersing taxa after controlling for topographic distance; (2) topographic distance was significantly correlated with the composition of moderate dispersers while accounting for geographical distance; and (3) topographic and perennial distances were correlated with the composition of moderate dispersers while controlling for each other (Table 7.4). Of all the models, local drivers (habitat distance plus flow regime distance) demonstrated the strongest relationships (i.e. the lowest AIC for single variable models) with the composition of weak, local and strong dispersers, while regional drivers (geographical, topographic, perennial and network distances) best-explained moderate dispersers (Table 7.4).

Table 7.2 Adjusted R^2 values, *F* statistic and *P*-value for each combination of aquatic invertebrate dispersal category (weak, local, moderate, and strong) and explanatory environmental (habitat distance and flow regime distance) and spatial (geographical, topographic, perennial and network distances) variables. Bonferroni correction was used to adjust *P*-values for multiple comparisons. Significant relationships ($P < 0.05$) are shown in bold. Aquatic invertebrates were sampled in 28 sites across seven

dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA.

Explanatory variable	Weak			Local			Moderate			Strong		
	Adj R^2	F	P-value	Adj R^2	F	P-value	Adj R^2	F	P-value	Adj R^2	F	P-value
Habitat distance	0.13	51.1	**< 0.01**	0.36	195.1	**< 0.01**	0.08	33.3	**< 0.01**	0.15	61.1	**< 0.01**
Flow regime distance	0.09	37.2	**< 0.01**	0.25	119.8	**< 0.01**	0.08	29.6	**< 0.01**	0.11	46.4	**< 0.01**
Geographical distance	0	2.4	0.120	0.03	10.5	**0.001**	0.07	29.1	**< 0.01**	0.09	37.7	**< 0.01**
Topographic distance	0	0	0.964	0.06	25.3	**< 0.01**	0.24	109.2	**< 0.01**	0.02	9.6	**0.002**
Perennial distance	0.02	8	**0.005**	0.1	40.9	**< 0.01**	0.27	129.3	**< 0.01**	0.01	5.6	**0.019**
Network distance	0	1.7	0.195	0	0.6	0.457	0	0.1	0.788	0	0.5	0.481

Figure 7.3 Pairwise correlations among all local and landscape distance metrics calculated between 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA. HAB, habitat distance; GEO, geographical distance; TOP, topographic distance; FLO, flow regime distance; NTW, network distance; PRN, perennial distance. Blue indicates a positive correlation, while red indicates a negative correlation. The intensity of the colour indicates the strength of the correlation. Spearman's ρ values are shown inside each box. * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$.
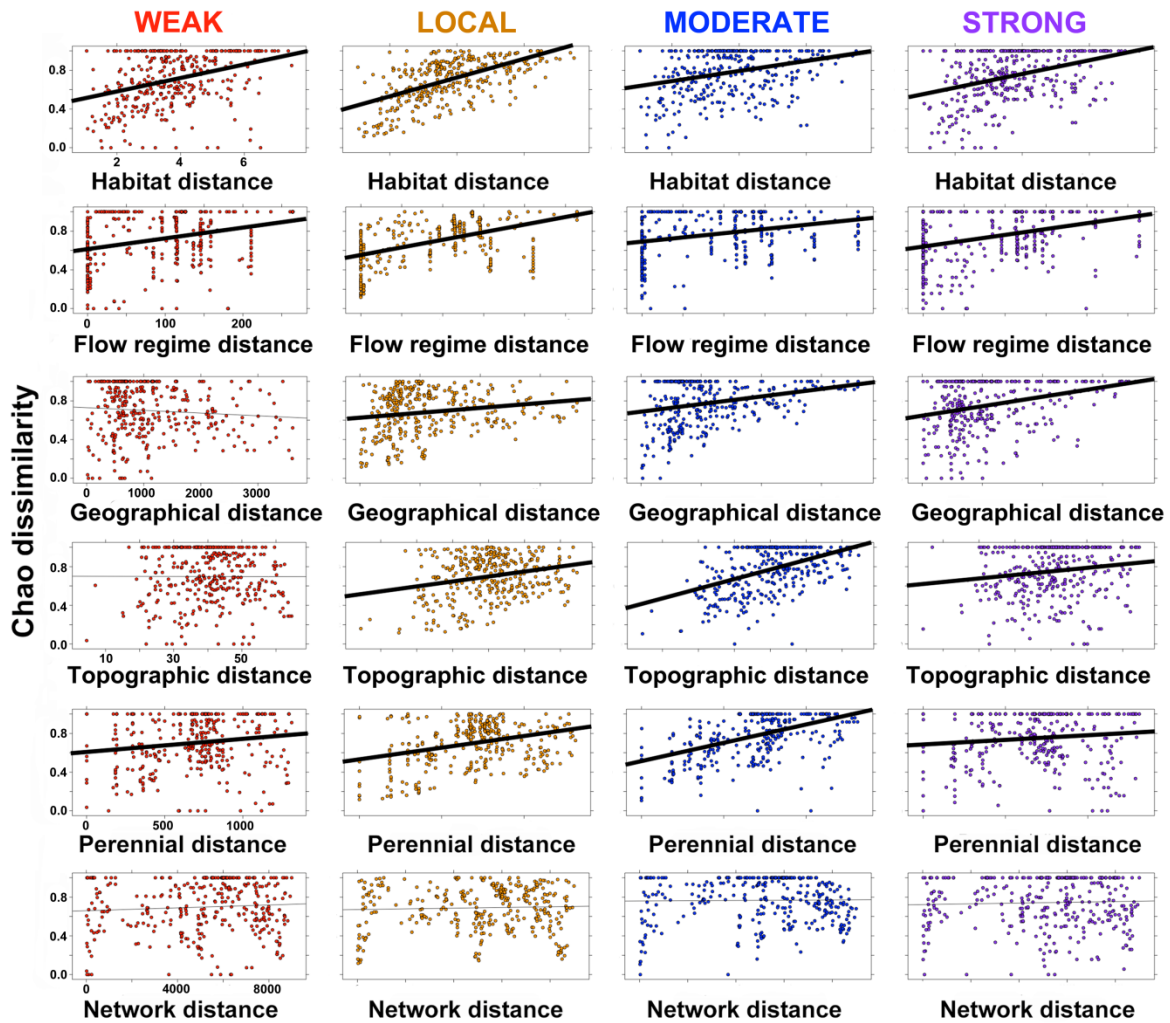
Figure 7.4 Distance decay relationships for each dispersal group of stream invertebrates sampled at 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA. WEAK, weak dispersers; LOCAL, local dispersers; MODERATE, moderate dispersers; STRONG, strong dispersers.

Table 7.3 Partial Mantel test results among those distance metrics that showed strong correlation between each other (Figure 3.3). GEO, geographical distance; TOP, topographic distance; PRN, perennial distance. * $0.01 < P < 0.05$; ** $P < 0.01$; n.s., not significant. Distances were calculated for 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA.

Comparison	Control matrix	r	P
Weak dispersers vs. GEO	TOP	−0.12	n.s.
Local dispersers vs. GEO	TOP	−0.02	n.s.
Moderate dispersers vs. GEO	TOP	−0.11	n.s.
Strong dispersers vs. GEO	TOP	0.28	**
Weak dispersers vs. TOP	GEO	0.08	n.s.
Local dispersers vs. TOP	GEO	0.2	n.s.
Moderate dispersers vs. TOP	GEO	0.43	**
Strong dispersers vs. TOP	GEO	−0.09	n.s.
Weak dispersers vs. PRN	TOP	0.19	n.s.
Local dispersers vs. PRN	TOP	0.22	n.s.
Moderate dispersers vs. PRN	TOP	0.33	**
Strong dispersers vs. PRN	TOP	0.04	n.s.
Weak dispersers vs. TOP	PRN	−0.11	n.s.
Local dispersers vs. TOP	PRN	0.09	n.s.
Moderate dispersers vs. TOP	PRN	0.26	*
Strong dispersers vs. TOP	PRN	0.11	n.s.

Table 7.4 ΔAIC (Akaike's information criterion) and weight for single variable models and the combinations (in italics) of habitat distance and flow regime distance (local distance metrics) and geographical, topographic, perennial and network distances (regional distance metrics). The lower the AIC, the higher the explanatory power of the model for each of the four invertebrate dispersal categories (weak, local, moderate and strong). Lowest AIC of single variables and combinations of variables for each dispersal category are marked in bold. Aquatic invertebrates were sampled in 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA.

Variable	Weak		Local		Moderate		Strong	
	ΔAIC	Weight	ΔAIC	Weight	ΔAIC	Weight	ΔAIC	Weight
Habitat distance	**15**	< 0.001	**60**	< 0.001	98	< 0.001	**20**	< 0.001
Flow regime distance	27	< 0.001	112	< 0.001	102	< 0.001	32	< 0.001
Geographical distance	60	< 0.001	205	< 0.001	102	< 0.001	40	< 0.001
Topographic distance	63	< 0.001	191	< 0.001	35	< 0.001	67	< 0.001
Perennial distance	55	< 0.001	177	< 0.001	**20**	< 0.001	71	< 0.001
Network distance	61	< 0.001	215	< 0.001	130	< 0.001	76	< 0.001
Local drivers	**0**	1	**0**	1	86	< 0.001	**0**	1
Regional drivers	53	< 0.001	179	< 0.001	**0**	1	37	< 0.001
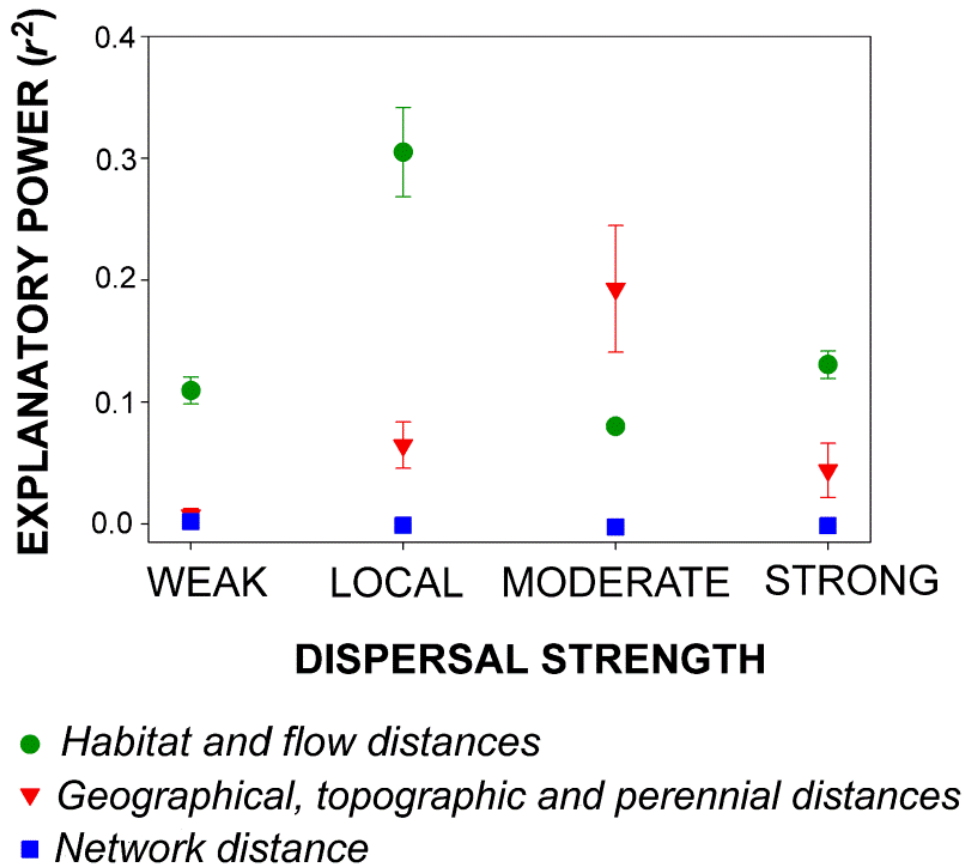
Figure 7.5 Explanatory power of three different groups of distance metrics over stream invertebrates' community dissimilarity among 28 sites across seven dryland streams distributed within a 400-km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA. Groups of distances: (a) habitat and flow distances; (b) geographical, topographic and perennial distances; and (c) network distance. Group (a) represents local environmental filters and group (b) represents regional landscape filters. The network distance is shown separately as having a very low power to predict community dissimilarity. The explanatory power is plotted against different categories of dispersal strength of stream invertebrates: weak, local, moderate and strong (see Materials and Methods section for a description of each category).

7.6   Discussion

We used distance decay relationships to examine the importance of local and regional drivers of aquatic invertebrate meta-community structure in dryland streams. DDRs have been used to examine the interaction of processes operating at local and regional scales for a wide range of organisms and ecosystems (Cottenie, 2005; Soininen *et al.*, 2007), including stream networks (Thompson & Townsend, 2006; Leprieur *et al.*, 2009; Brown & Swan, 2010; Warfe *et al.*, 2013). However, past studies have largely not explored the relative roles of local- and regional-scale landscape drivers within connected networks. The only published study that used DDRs to

address the effect of hydrological connectivity on stream meta-communities showed, rather counter-intuitively, that the loss of connectivity enhanced DDR in a variety of organisms (Warfe *et al.*, 2013). However, environmental conditions in that study were not independent of geographical distance; therefore dispersal limitation and niche partitioning both played a role in shaping assemblage structure. Our results suggest that fragmentation impacts DDRs by altering the viable dispersal pathways, with organisms dispersing overland instead of using the stream network. As we hypothesized, meta-community structure was determined by three main factors: niche filtering due to local among-habitat differences, dispersal ability of the species, and landscape resistance (geographical distance, topography and availability of perennial refugia). Notably, we did not examine the influence of biotic interactions on invertebrate community composition for a number of reasons. First, our study streams do not contain predator fish species, and similarly predation effects from amphibians (tadpoles) and invertebrate beetles are minimal. Second, as supported by ecological theory and substantial empirical evidence, invertebrate communities in harsh intermittent streams such as those examined here are predominantly shaped by environmental factors (Bogan *et al*., 2013), whereas biological drivers play a more important role in environmentally-benign streams (Jackson *et al.,* 2001).

Niche filtering due to among-habitat differences. We hypothesized that high environmental heterogeneity would generate significant environmental DDRs for all dispersal categories. Indeed, we found that the local filters of habitat and flow regime had a stronger effect on community dissimilarity than regional filters across all dispersal classes, except for moderate dispersers. At intermediate levels of dispersal, organisms might be able to survive harsh environmental conditions such as floods and droughts by escaping and finding refugia (Velasco & Millan, 1998; Lytle, 1999), but at the same time they might not be able to reach all the available habitats, preventing meta-community homogenization via mass effects (Kneitel & Miller, 2003; Leibold *et al.*, 2004). The significant influence of local filters on meta-community patterns was not surprising given the high temporal and spatial variation in environmental conditions in the study region. Highly variable seasonal and interannual precipitation patterns and various geomorphic settings (e.g. bedrock canyons, alluvial fans) interact to create a patchy stream landscape. In these dryland streams, perennial reaches are adjacent to intermittent reaches, and intermittent reaches with seasonal flow in a wet year can be completely dry during the same period in a dry year (Jaeger & Olden, 2012; Bogan *et al*., 2013). The amount of water and how it is distributed within the year (i.e. frequency and timing of droughts and floods) have important consequences for water quality and habitat variables (e.g. canopy cover, river substratum). Accordingly, these local habitat filters should be extremely strong in dryland streams. Our results validate previous studies that linked these patchy environmental conditions to disruptions in the longitudinal patterns of stream invertebrate communities in the region (Bogan *et al.*, 2013). They are also in agreement with a recent study from north-western Australia, which found that flow and channel width best explained invertebrate meta-community

patterns across a range of perennial and intermittent streams (Warfe *et al.*, 2013). Moreover, the importance of niche filtering in structuring meta-communities has been demonstrated for a variety of ecosystems (Soininen *et al.*, 2007), including ponds (Urban, 2004; Chase, 2007) and streams (Thompson & Townsend, 2006; Brown & Swan, 2010). As the loss of connectivity among stream reaches results from high flow heterogeneity (leading to high environmental heterogeneity), niche filtering can be expected to be strong in fragmented stream networks.

Dispersal ability. Aquatic invertebrates are known to have very different dispersal capacities, ranging from a few metres to thousands of kilometres (Kovats *et al.*, 1996; Bilton *et al.*, 2001; McCauley, 2006). Given that meta-community structure is highly dependent on geographical scale (Brown *et al.*, 2011; Maloney & Munguia, 2011; Nekola & McGill, 2014), differences in dispersal can be expected to affect DDRs (Nekola & White, 1999). Increasing dispersal ability is expected to enhance community similarity among sites and reduce beta diversity among habitat patches (Shurin *et al.*, 2009). Recent studies on invertebrate meta-communities in stream networks have provided evidence for this pattern, with DDR being weakened by increasing dispersal strength (Thompson & Townsend, 2006; Brown & Swan, 2010; Bonada *et al*., 2012). However, we found a more complex unimodal pattern, with DDR peaking at intermediate dispersal strength for different measures of landscape resistance. This pattern might result from assemblages of weak dispersers showing no spatial structure as a result of dispersal limitation while assemblages of strong dispersers are more homogeneous across the landscape as a result of the absence of dispersal restrictions (Kneitel & Miller, 2003; Leibold *et al.*, 2004). Figure 7.5 illustrates this pattern by showing the explanatory power of local (habitat and flow distances) and landscape (geographical distance, topography and availability of perennial refugia) filters along the dispersal strength gradient.

Our results could be influenced by the lower flow connectivity and environmental stability in our dryland study system compared to more mesic stream systems. In low connectivity systems, weak dispersers are highly isolated, leading to species distributions ruled by ecological drift and niche filtering (Hu *et al.*, 2006). Therefore, in these fragmented systems, low connectivity coupled with differing environmental conditions can lead to adjacent sites having very different assemblages of weak dispersal species. Previous investigations on the flightless aquatic obligate *Abedus herberti* within our study area reported strong population genetic structure, with populations within the same stream drainage (less than 5 km apart) showing significant genetic differentiation (Finn *et al.*, 2007; Phillipsen & Lytle, 2013). This same pattern has been observed for the blackfly *Prosimulium neomacropyga* in isolated alpine headwater streams (Finn & Poff, 2011). On the other side of the spectrum, extremely strong dispersers can break down geographical barriers, occurring in all suitable habitats (Townsend *et al.*, 2003; McCauley, 2006; Thompson & Townsend, 2006; Brown & Swan, 2010; Bonada *et al.*, 2012). This would explain the decrease in the explanatory power of landscape variables over meta-community structure at the upper end of the dispersal strength gradient in the present study (Figure 7.5). We suggest that regional drivers should be important predictors of meta-community structure up to a certain

dispersal distance threshold, beyond which dispersal is strong enough to break the limitation imposed by geographical barriers.

Distance among sites. Network distance did not significantly affect community dissimilarity for any of the four dispersal groups, as we hypothesized. This contradicts the general rule of aquatic invertebrates using the stream network as the main 'highway' for dispersal (Petersen *et al.*, 2004). While evidence supporting the ideas of the stream channel as the primary dispersal route and restricted overland dispersal between catchments continue to accumulate in the literature (Hughes, 2007; Brown & Swan, 2010; Rouquette *et al.*, 2013), previous investigations within our study area suggest that dryland streams might be exceptions to this rule. Many aquatic invertebrate species in our study region disperse laterally from stream corridors in search of other wetted habitats (Bogan & Boersma, 2012). Additionally, Bogan *et al.* (2013) reported an interruption of the river continuum, where invertebrate communities in distant headwater and lowland perennial streams were more similar to one another than to those in intervening intermittent reaches. Furthermore, Phillipsen & Lytle (2013) found no significant relationship between network distance and population genetic structure of *Abedus herberti.* Instead, they found that topography best explained genetic structure and suggested that overland dispersal resulted from flood-escape behaviour (Lytle, 1999; Lytle *et al.*, 2008), where individuals crawl from streams during floods and accidentally end up in adjacent drainages.

We found significant (but generally weak) DDRs for perennial habitat distance in all cases and for topographic distance in all cases except weak dispersers. This supports the hypothesis of overland dispersal (flight and crawling) being the main dispersal pathway for aquatic invertebrates in highly fragmented stream networks, such as those inhabiting dryland regions. Similarly, Campbell Grant *et al.* (2010) found evidence of high overland dispersal rates in newly metamorphosed juveniles of stream salamanders and suggested that the salamanders followed that dispersal strategy to increase population persistence across isolated headwater streams.

7.7   Conclusions

Our DDR analyses suggest that in highly heterogeneous stream networks, where environmental conditions vary greatly across space and time, local factors (i.e. niche filtering) may swamp regional influences (i.e. landscape filters) on aquatic invertebrate meta-community structure. However, this interaction between local and regional factors is dependent on species' dispersal capacity, which determines their ability to colonize suitable habitats. Using a combination of landscape and local distance measures, we found evidence that local and weak dispersers were affected by local-scale factors, intermediate dispersers were affected by landscape-level factors, and strong dispersers showed no discernable pattern. This resulted in a hump-shaped relationship between dispersal ability and landscape-level factors, where only moderate dispersers showed significant DDRs. Stream corridors may not be a primary dispersal pathway in these networks, where frequent drought and flood disturbances generate habitat patches with low connectivity.

Overland pathways, using perennial refugia as stepping-stones, might be the main dispersal route for aquatic invertebrates in these dryland stream networks (Phillipsen & Lytle, 2013).

Our DDR approach has the potential to generate timely management insights, such as the importance of preserving perennial habitat patches in fragmented river networks. Meta-communities of weak dispersal species are highly disconnected in dryland stream networks. As most of these species depend on perennial water sources for their survival (Bogan & Lytle, 2011; Hermoso *et al.*, 2013), intensifying droughts may have effects at both meta-population and meta-community levels. Our results suggest that perennial habitat patches may facilitate dispersal of aquatic invertebrates and thereby may ensure the long-term viability of populations. Conserving perennial habitats is of vital importance in dryland streams, and it will become increasingly important in basins experiencing flow reduction due to warmer temperatures and increased anthropogenic water use (Marshall *et al.*, 2010). Given the different responses of invertebrate meta-communities to our various geographical and environmental distance measures, we encourage future investigations to incorporate multiple regionally relevant measures of landscape resistance into their studies. Further research is needed to better understand how environmental stability affects the balance between local and regional factors structuring meta-community patterns in dendritic networks, including work at different spatial scales and degrees of fragmentation.

7.8 Acknowledgements

7.9 Appendix A

Aquatic invertebrate taxa list (sampled in 28 sites across seven dryland streams distributed within a 400 km^2 section of the Upper San Pedro River basin, south-eastern Arizona, USA) including their assignation into one of four dispersal categories: weak, local, moderate and strong dispersers.

Order	Family	Genus/Species	Dispersal Category

Acariformes	Acari	Acari	Weak
Amphipoda	Crustacea	*Hyalella*	Weak
Annelida	Hirudinea	Hirudinea	Weak
Anostraca	Anostraca	Anostraca	Weak
Basommatophora	Ancylidae	*Ferrissia*	Weak
Basommatophora	Ansylidae	Ancylidae	Weak
Decapoda	Cambaridae	Procambarus	Weak
Diplostraca	Limnadiidae	Eulimnadia	Weak
Gastropoda	Hydrobiidae	*Pyrgulopsis*	Weak
Gastropoda	Lymnaeidae	Lymnaeidae	Weak
Gastropoda	Physidae	Physidae	Weak
Gastropoda	Planorbidae	Planorbidae	Weak
Hemiptera	Belostomatidae	*Abedus herberti*	Weak
Hemiptera	Nepidae	*Curicta pronotata*	Weak
Platyhelmenthes	Platyhelmenthes	Platyhelmenthes	Weak
Podocopida	Ostracoda	Ostracoda	Weak
veneroida	Sphaeriidae	*Pisidium*	Weak
Coleoptera	Dryopidae	*Helichus lithophilus*	Local
Coleoptera	Dryopidae	*Helichus suturalis*	Local
Coleoptera	Dryopidae	*Helichus triangularis*	Local
Coleoptera	Dryopidae	*Postelichus confluentus*	Local
Coleoptera	Dryopidae	*Postelichus immsi*	Local
Coleoptera	Elmidae	*Heterelmis*	Local
Coleoptera	Elmidae	*Microcylloepus*	Local

Coleoptera	Elmidae	*Optioservus*	Local
Coleoptera	Elmidae	*Zaitzevia*	Local
Coleoptera	Hydraenidae	*Gymnochthebius*	Local
Coleoptera	Hydrophilidae	*Chaetarthria*	Local
Diptera	Ceratopogonidae	*Atrichopogon*	Local
Diptera	Ceratopogonidae	*Ceratopogoninae*	Local
Diptera	Ceratopogonidae	*Forcipomyia*	Local
Diptera	Chironomidae	*Ablabesmyia*	Local
Diptera	Chironomidae	*Acricotopus*	Local
Diptera	Chironomidae	*Apedilum*	Local
Diptera	Chironomidae	*Apsectrotanypus*	Local
Diptera	Chironomidae	*Brillia*	Local
Diptera	Chironomidae	*Bryophaenocladius*	Local
Diptera	Chironomidae	*Chaetocladius*	Local
Diptera	Chironomidae	*Parachaetocladius*	Local
Diptera	Chironomidae	*Paracladopelma*	Local
Diptera	Chironomidae	*Corynoneura*	Local
Diptera	Chironomidae	*Paracricotopus*	Local
Diptera	Chironomidae	*Cricotopus-Orthocladius*	Local
Diptera	Chironomidae	*Cryptochironomus*	Local
Diptera	Chironomidae	*Demicryptochironomus*	Local
Diptera	Chironomidae	*Diamesa*	Local
Diptera	Chironomidae	*Dicrotendipes*	Local
Diptera	Chironomidae	*Heleniella*	Local
Diptera	Chironomidae	*Heterotrissocladius*	Local

Diptera	Chironomidae	*Hydrobaenus*	Local
Diptera	Chironomidae	*Parakiefferella*	Local
Diptera	Chironomidae	*Krenosmittia*	Local
Diptera	Chironomidae	*Labrundinia*	Local
Diptera	Chironomidae	*Larsia*	Local
Diptera	Chironomidae	*Limnophyes*	Local
Diptera	Chironomidae	*Lopescladius*	Local
Diptera	Chironomidae	*Paramerina*	Local
Diptera	Chironomidae	*Mesosmittia*	Local
Diptera	Chironomidae	*Parametriocnemus*	Local
Diptera	Chironomidae	*Micropsectra*	Local
Diptera	Chironomidae	*Nanocladius*	Local
Diptera	Chironomidae	*Nilotanypus*	Local
Diptera	Chironomidae	*Parochlus*	Local
Diptera	Chironomidae	*Pentaneura*	Local
Diptera	Chironomidae	*Phaenopsectra*	Local
Diptera	Chironomidae	*Polypedilum*	Local
Diptera	Chironomidae	*Procladius*	Local
Diptera	Chironomidae	*Psectrocladius*	Local
Diptera	Chironomidae	*Pseudosmittia*	Local
Diptera	Chironomidae	*Pseudochironomus*	Local
Diptera	Chironomidae	*Rheocricotopus*	Local
Diptera	Chironomidae	*Rheotanytarsus*	Local
Diptera	Chironomidae	*Chironomus*	Local
Diptera	Chironomidae	*Saetheria*	Local

Diptera	Chironomidae	*Parasmittia*	Local
Diptera	Chironomidae	*Smittia*	Local
Diptera	Chironomidae	*Stempellinella*	Local
Diptera	Chironomidae	*Stictochironomus*	Local
Diptera	Chironomidae	*Stenochironomus*	Local
Diptera	Chironomidae	*Tanytarsus*	Local
Diptera	Chironomidae	*Paratanytarsus*	Local
Diptera	Chironomidae	*Paratendipes*	Local
Diptera	Chironomidae	*Virgatanytarsus*	Local
Diptera	Chironomidae	*Eukiefferiella brehmi*	Local
Diptera	Chironomidae	*Eukiefferiella claripennis*	Local
Diptera	Chironomidae	*Eukiefferiella coerulescens*	Local
Diptera	Chironomidae	*Eukiefferiella devonica*	Local
Diptera	Chironomidae	*Eukiefferiella gracei*	Local
Diptera	Chironomidae	*Eukiefferiella rectangularis*	Local
Diptera	Chironomidae	*Microtendipes pedellus* grp.	Local
Diptera	Chironomidae	*Thienemanniella fusca*	Local
Diptera	Chironomidae	*Thienemannimyia* grp.	Local
Diptera	Chironomidae	*Thienemanniella xena*	Local
Diptera	Chironomidae	*Tvetenia bavarica* grp.	Local
Diptera	Culicidae	*Aedes*	Local
Diptera	Culicidae	*Anopheles*	Local
Diptera	Culicidae	*Culex*	Local
Diptera	Culicidae	*Culiseta*	Local
Diptera	Culicidae	*Psorophora*	Local

Diptera	Dixidae	*Dixa*	Local
Diptera	Dixidae	*Dixella*	Local
Diptera	Dolichopodidae	Dolichopodidae	Local
Diptera	Empididae	Empididae	Local
Diptera	Ephydridae	Ephydridae	Local
Diptera	Muscidae	Muscidae	Local
Diptera	Psychodidae	*Maruina*	Local
Diptera	Psychodidae	*Pericoma*	Local
Diptera	Ptychopteridae	*Ptychoptera*	Local
Diptera	Simuliidae	*Prosimulium*	Local
Diptera	Simuliidae	*Simulium*	Local
Diptera	Stratiomyidae	*Caloparyphus*	Local
Diptera	Stratiomyidae	*Euparyphus*	Local
Diptera	Syrphidae	Syrphidae	Local
Diptera	Tabanidae	*Tabanus*	Local
Diptera	Thaumaleidae	Thaumaleidae	Local
Diptera	Tipulidae	*Antocha*	Local
Diptera	Tipulidae	*Dicranota*	Local
Diptera	Tipulidae	*Limnophila*	Local
Diptera	Tipulidae	*Limonia*	Local
Diptera	Tipulidae	*Pedicia*	Local
Diptera	Tipulidae	*Tipula*	Local
Ephemeroptera	Ameletidae	*Ameletus*	Local
Ephemeroptera	Baetidae	*Acentrella*	Local
Ephemeroptera	Baetidae	*Baetis*	Local

Ephemeroptera	Baetidae	*Callibaetis*	Local
Ephemeroptera	Baetidae	*Camelobaetidius maidu*	Local
Ephemeroptera	Baetidae	*Fallceon*	Local
Ephemeroptera	Caenidae	*Caenis*	Local
Ephemeroptera	Heptageniidae	*Ecdyonourus*	Local
Ephemeroptera	Leptohyphidae	*Homoleptohyphes*	Local
Ephemeroptera	Leptohyphidae	*Tricorythodes*	Local
Ephemeroptera	Leptophlebiidae	*Choroterpes*	Local
Ephemeroptera	Leptophlebiidae	*Farrodes*	Local
Hemiptera	Hebridae	*Hebrus*	Local
Lepidoptera	Crambidae	*Petrophila*	Local
Plecoptera	Capniidae	*Capnia*	Local
Plecoptera	Capniidae	*Mesocapnia*	Local
Plecoptera	Chloroperlidae	Chloroperlidae	Local
Plecoptera	Chloroperlidae	*Sweltsa*	Local
Plecoptera	Nemouridae	*Malenka-Amphinemoura*	Local
Trichoptera	Brachycentridae	*Micrasema*	Local
Trichoptera	Calamoceratidae	*Phylloicus mexicanus*	Local
Trichoptera	Helicopsychidae	*Helicopsyche*	Local
Trichoptera	Hydrobiosidae	*Atopsyche*	Local
Trichoptera	Hydropsychidae	*Cheumatopsyche*	Local
Trichoptera	Hydropsychidae	*Hydropsyche*	Local
Trichoptera	Hydroptilidae	*Culoptila*	Local
Trichoptera	Hydroptilidae	*Metrichia*	Local
Trichoptera	Hydroptilidae	*Ochrotrichia*	Local

Trichoptera	Hydroptilidae	*Oxyethira*	Local
Trichoptera	Hydroptilidae	*Hydroptila*	Local
Trichoptera	Lepidostomatidae	*Lepidostoma acarolum*	Local
Trichoptera	Lepidostomatidae	*Lepidostoma sp.*	Local
Trichoptera	Leptoceridae	*Nectopsyche*	Local
Trichoptera	Leptoceridae	*Oecetis*	Local
Trichoptera	Limnephilidae	*Hesperophylax*	Local
Trichoptera	Philopotamidae	*Wormaldia*	Local
Trichoptera	Polycentropodidae	*Polycentropus*	Local
Trichoptera	Psychomyiidae	*Tinodes*	Local
Coleoptera	Dytiscidae	*Desmopachria portmanni*	Moderate
Coleoptera	Dytiscidae	Hydroporinae	Moderate
Coleoptera	Dytiscidae	*Hygrotus patruelis*	Moderate
Coleoptera	Dytiscidae	*Hygrotus wardi*	Moderate
Coleoptera	Dytiscidae	*Laccophilus fasciatus*	Moderate
Coleoptera	Dytiscidae	*Laccophilus maculosus*	Moderate
Coleoptera	Dytiscidae	*Laccophilus mexicanus*	Moderate
Coleoptera	Dytiscidae	*Laccophilus oscillator*	Moderate
Coleoptera	Dytiscidae	*Laccophilus pictus*	Moderate
Coleoptera	Dytiscidae	*Liodessus obscurellus*	Moderate
Coleoptera	Dytiscidae	*Neoclypeodytes cinctellus*	Moderate
Coleoptera	Dytiscidae	*Neoclypeodytes fryi*	Moderate
Coleoptera	Dytiscidae	*Neoporus*	Moderate
Coleoptera	Dytiscidae	*Rhantus atricolor*	Moderate
Coleoptera	Dytiscidae	*Rhantus gutticollis*	Moderate

Coleoptera	Dytiscidae	*Sanfilippodytes*	Moderate
Coleoptera	Dytiscidae	*Stictotarsus corvinus*	Moderate
Coleoptera	Dytiscidae	*Stictotarsus roffi*	Moderate
Coleoptera	Dytiscidae	*Boreonectes striatellus*	Moderate
Coleoptera	Dytiscidae	*Thermonectus marmoratus*	Moderate
Coleoptera	Dytiscidae	*Thermonectus nigrofasciatus*	Moderate
Coleoptera	Gyrinidae	*Gyrinus plicifer*	Moderate
Coleoptera	Haliplidae	*Peltodytes dispersus*	Moderate
Coleoptera	Haliplidae	*Peltodytes callosus*	Moderate
Coleoptera	Hydraenidae	*Hydraena*	Moderate
Coleoptera	Hydrophilidae	*Anacaena signaticollis*	Moderate
Coleoptera	Hydrophilidae	*Berosus miles*	Moderate
Coleoptera	Hydrophilidae	*Berosus punctatissimus*	Moderate
Coleoptera	Hydrophilidae	*Berosus rugulosus*	Moderate
Coleoptera	Hydrophilidae	*Berosus salvini*	Moderate
Coleoptera	Hydrophilidae	*Berosus stylifer*	Moderate
Coleoptera	Hydrophilidae	*Cymbiodyta*	Moderate
Coleoptera	Hydrophilidae	*Enochrus aridus*	Moderate
Coleoptera	Hydrophilidae	*Enochrus piceus glabrus*	Moderate
Coleoptera	Hydrophilidae	*Enochrus pygmaeus pectoralis*	Moderate
Coleoptera	Hydrophilidae	*Helophorus*	Moderate
Coleoptera	Hydrophilidae	*Hydrophilus*	Moderate
Coleoptera	Hydrophilidae	*Laccobius hardyi*	Moderate
Coleoptera	Hydrophilidae	*Tropisternus lateralis*	Moderate

Hemiptera	Belostomatidae	*Belostoma flumineum*	Moderate
Hemiptera	Corixidae	*Graptocorixa abdominalis*	Moderate
Hemiptera	Corixidae	*Graptocorixa serrulata*	Moderate
Hemiptera	Corixidae	*Graptocorixa gerhardi*	Moderate
Hemiptera	Corixidae	*Hesperocorixa*	Moderate
Hemiptera	Corixidae	*Rhamphocorixa acuminata*	Moderate
Hemiptera	Corixidae	*Trichocorixa uhleri*	Moderate
Hemiptera	Gerridae	*Aquarius remigis*	Moderate
Hemiptera	Notonectidae	*Buenoa arida*	Moderate
Hemiptera	Notonectidae	*Buenoa arizonis*	Moderate
Hemiptera	Notonectidae	*Buenoa margaritacea*	Moderate
Hemiptera	Notonectidae	*Buenoa scimitra*	Moderate
Hemiptera	Notonectidae	*Notonecta hoffmanni*	Moderate
Hemiptera	Veliidae	*Microvelia*	Moderate
Megaloptera	Corydalidae	*Corydalus texanus*	Moderate
Megaloptera	Corydalidae	*Neohermes*	Moderate
Odonata	Aeshnidae	*Oplonaeschna armata*	Moderate
Odonata	Calopterygidae	*Hetaerina*	Moderate
Odonata	Coenagrionidae	*Argia*	Moderate
Odonata	Coenagrionidae	*Coenagrion / Enallagma*	Moderate
Odonata	Gomphidae	*Erpetogomphus*	Moderate
Odonata	Lestidae	*Archilestes grandis*	Moderate
Odonata	Libellulidae	*Brechmorhoga*	Moderate
Odonata	Libellulidae	*Pantala hymenaea*	Moderate
Odonata	Libellulidae	*Sympetrum*	Moderate

Coleoptera	Dytiscidae	*Agabus*	Strong
Coleoptera	Dytiscidae	*Boreonectes aequinoctialis*	Strong
Coleoptera	Gyrinidae	*Dineutus sublineatus*	Strong
Coleoptera	Hydrophilidae	*Tropisternus affinis*	Strong
Hemiptera	Belostomatidae	*Lethocerus medius*	Strong
Hemiptera	Nepidae	*Ranatra quadridentata*	Strong
Hemiptera	Notonectidae	*Notonecta lobata*	Strong
Odonata	Cordulegastridae	*Cordulegaster diadema*	Strong
Odonata	Libellulidae	*Libellula saturata*	Strong
Odonata	Libellulidae	*Paltothemis lineatipes*	Strong

8 Convergent diversity and trait composition in temporary streams and ponds

Synopsis: This chapter takes some of the general concepts developed above, specifically how functional diversity relates to specific niche-based traits such as hydrologic requirements, and asks whether these concepts can be applied to other systems. We find that systems as different as aridland streams and mesic forest ponds have similar trait-space patterns, especially when we consider insect communities occupying intermittent habitats. Hydrology is essentially a strong environmental filter that determines the types of traits (and thus species) that can occur in any particular habitat. Thus, our many of our findings may be relevant to the management of ecosystems beyond the aridland biome.

8.1 Abstract

Hydrology is the main environmental filter in aquatic ecosystems and may result in shared tolerances and functional traits among disparate ecosystems. We analyzed the associations between taxonomic and functional facets of diversity within aquatic ecosystems (ponds vs. streams) across a hydroperiod gradient (1 to 365 days) to untangle the hydrologic drivers of aquatic invertebrate diversity. We used invertebrate assemblage data from 7 arid-land streams in southeastern Arizona, USA collected over 2 years and 9 temperate woodland ponds in Ontario, Canada collected over 2 years. Our results showed that although invertebrate assemblages from streams and ponds differ taxonomically, hydroperiod had similar influence on invertebrate trait structure regardless of biogeographic and habitat differences. Streams and ponds independently showed strong positive relationships between functional richness and taxonomic richness; however the relationship was weaker in ponds, indicating higher functional redundancy. Intermittent ponds and streams tended to have lower functional and taxonomic richness than their perennial counterparts, but harbored greater beta diversity. Our results suggest that even though ponds and streams are fundamentally different habitats with distinct faunas and unique ecological processes, hydrology produces convergent patterns in both trait composition and diversity patterns.

8.2 Introduction

Environmental filtering is the process by which a subset of the regional species pool can persist in a local habitat because these species have particular traits or phenotypes suited to local environmental conditions (Southwood 1988, Poff 1997). Filtering works on the principle that species differ in their environmental requirements and tolerances. Communities that have different compositions of species are likely to have different trait diversity. Functional diversity is defined as the range of species and traits that influence ecosystem functioning (Tilman 2001). Taxonomic richness and functional richness may respond differently to environmental gradients depending on the composition of the community (e.g., dominance of generalists or functional

redundant species) (Villéger et al. 2012). Additionally, beta diversity – both 'turnover' and 'variation' beta (Anderson et al. 2011) – may be a more informative measure of the effects of environmental variation than taxonomic richness alone. Variation beta diversity is defined as variation in species composition among sampling locations and turnover beta diversity measures change in community structure along a particular gradient. Thus, characterizing and comparing the relationship between taxonomic and functional richness across multiple aquatic ecosystems and environmental gradients provides insights into community organization and ecosystem function.

Hydroperiod or flow duration describes the length of the aquatic phase over the course of a year, and is a central organizing component of freshwater ecosystems. Hydrology has been a long-standing focus of both running (lotic)- and still (lentic)-water research because of its powerful role in shaping the ecology and evolution of species (Wissinger 1999, Brooks 2000, Lytle and Poff 2004) as well as ecosystem processes (Sparks 1995). Variation in pond hydroperiod (Wiggins et al. 1980, Semlitsch et al. 1996, Skelly 1996, Wellborn et al. 1996, Urban 2004) and stream flow duration (Poff and Ward 1989, Poff et al. 1997, Lamouroux et al. 2002, Vieira et al. 2004, Hoeinghaus et al. 2007) influences invertebrate and vertebrate species richness and composition, predator distribution, and reproductive success. Historical and current hydrologic regimes play a central role in regulating ecological processes at the species, trait and community, and ecosystem levels (Resh et al. 1988, Poff et al. 1997, Church 2008, Konar et al. 2013).

Researchers studying either ponds or streams have independently identified hydrology as a primary driver of ecological communities in freshwater ecosystems. Yet studies that make comparisons across the lotic-lentic divide are exceptionally rare (Williams et al. 2003, Wurtsbaugh et al. 2015). Because ponds and streams have fundamentally different key ecosystem properties, (i.e., branching pattern, flow, sedimentation, disturbance, water chemistry) one might expect ecological patterns and processes to differ. However, if a particular environmental gradient is driving processes equally in both ecosystems, we might expect ecological congruence between ponds and streams. For instance, it is possible that similar patterns (i.e., species richness, community composition, functional traits, and ecosystem properties) result from a common hydrologic filter that operates similarly in both ponds and streams. If this is the case, we predict that because of evolved life-history strategies due to a common environmental gradient (Southwood 1977), that a subset of traits will be shared among the different organisms that inhabit ponds vs. streams.

We took a functional trait perspective to compare invertebrate assemblages from woodland ponds in SE Ontario, Canada to arid-land streams in SE Arizona, U.S.A. that experience similar hydroperiod gradients. In this study we hypothesized that habitats with similar hydrologic conditions, regardless of ecosystem type, should share species traits. We hypothesized that functional richness should be positively related to taxonomic richness in both ponds and streams and that ponds and streams should show similar richness patterns along a hydrologic gradient. We predicted higher taxonomic richness and functional richness in perennial ponds and streams

vs. their intermittent counterparts. Additionally, we predicted that beta diversity (turnover) should decline along a gradient of long to short hydroperiod and that variation beta diversity should be higher in intermittent stream reaches and ponds because disturbance and isolation can promote higher beta diversity.

8.3   Methods

Survey of aquatic invertebrate communities. We compared invertebrate assemblages collected along a hydroperiod gradient from temperate ponds (Ontario, Canada) and dryland streams (Arizona, USA). The seasons of sampling are different between ponds and streams, but they represent the main active aquatic seasons in each habitat. Each month from April to September in 2008 and 2009, we collected aquatic invertebrates by dip-net (500 µm mesh) from fishless ponds that spanned a natural gradient from intermittent freshwater woodland ponds to perennial freshwater marshes at the Queen's University Biological Station (QUBS), Ontario, Canada (Schriever and Williams 2013). Samples were collected at several locations throughout each pond. Seven ponds were used in 2008 with two other ponds added to the study in 2009 ($n = 9$ ponds, total 80 collections). Pond invertebrate samples were sorted into major insect groups in the field, placed in plastic jars, and held on ice until deposited in a freezer. In the laboratory, we identified pond invertebrates to genus level (some family and species level identifications) with a dissecting microscope.

We collected aquatic invertebrates from 23 sites distributed across 7 arid-land streams in the Huachuca Mountains within the Upper San Pedro River Basin of southeastern Arizona, USA (Schriever et al. 2015). All streams are fishless except for the San Pedro River; however, no fish were collected in our sampling effort. We distributed our sample sites among perennial, intermittent and ephemeral reaches (classification follows Levick et al. 2008). Sites were sampled multiple times between 2009 and 2011, and most sampling occurred during the fall and winter seasons (November and December; March and April, respectively, total 120 collections). These seasons represent a time when streams generally have flow. Riffle samples consisted of scrubbing rocks and agitating stream bed substrates in a 1 m^2 area, and dislodged macroinvertebrates were collected in a downstream dip-net. A pool sample consisted of a time x area standardized collection of the entire pool area using a dip-net at 10 seconds for every 1 m^2 area of pool. Stream invertebrate samples were preserved in 95% ethanol and identified in the laboratory to genus or species for insects (including Chironomidae) and family or order for non-insects.

Measuring hydroperiod. The hydroperiod of each pond was measured as the duration of the aquatic phase or days from ice-off until each pond dried, as recorded in 2008 and 2009. Each pond was visited bi-weekly to check depth and presence of water. In the Arizona streams, we measured flow regime through the deployment of 15 wet/dry electrical resistance (ER) sensors (Jaeger and Olden 2012) to quantify duration of stream flow near stream invertebrate sampling locations. The sensors logged relative conductivity at 15 minute intervals from 15 April 2010 to

31 December 2011 as a proxy for the presence of surface water. From these conductivity data we calculated the hydroperiod for each year of sample for each sampling site using the nearest sensor by summing 15-minute time periods of both wet and dry conditions for the sampling period, converting the time units to days. Ponds and stream sites were grouped using ER data into two hydrologic categories, intermittent or perennial.

Trait data and analysis. We used a trait matrix developed by Schriever et al. (2015) for the AZ stream invertebrates and developed another for the pond invertebrates by using publications of primary literature, databases, and expert knowledge to define trait states. We selected seven traits (30 states) that are associated with biological responses to drought in arid-land streams and that describe functional composition of invertebrate communities: respiration, voltinism, primary locomotion and habit, diapause, dispersal capability, body size, and functional feeding group (Boersma et al. 2014, Schriever et al. 2015). We found sufficient trait information for 88 freshwater macroinvertebrate taxa (out of 94 identified taxa) collected from study ponds and 211 taxa from study streams (out of 225 identified) (Appendix A and Appendix S1 in Schriever et al. 2015). Only taxa with sufficient trait data were used to calculate functional richness for each pond and stream community. Functional richness (FRic) measures the volume of functional space occupied by a community in a multivariate trait space (Cornwell et al. 2006, Villéger et al. 2008). FRic was calculated using the R-based FD package (R Core Team 2013) and the function dbFD (Laliberté and Legendre 2010, Laliberté and Shipley 2011). Traits were given equal weights, and standardized to mean 0 and unit variance. Taxonomic richness was calculated as the number of unique taxa identified at each site.

Statistical analysis. We performed a Redundancy Analysis (RDA) to test for the influence of ecosystem and hydroperiod factors on trait structure. RDA is a direct gradient ordination method that tests if trait composition is related to sampling site and any constraining environmental variables. The constraining variables were ecosystem (pond or stream) and hydroperiod (continuous variable; number of days) and the response variables were the 30 trait states. We multiplied the species x traits matrix (88 pond taxa and 211 stream taxa x 30 possible trait states) by the species incidence x sites matrix (88 taxa x 16 pond sites; 211 taxa x 23 stream sites) to arrive at a traits x sites matrix (30 traits x 39 sites), which we used, untransformed, as input in RDA along with the constraining variables. This approach allowed us toshow how pond and stream sites are characterized by particular environmental variables and whether particular traits can be attributed to a specific measured predictor variable (Gotelli and Ellison 2004). We conducted permutation tests on the RDA models to test the significance of constraining variables based on 1000 randomizations. Additionally, we performed a multivariate nonparametric ANOVA of dissimilarities (PERMANOVA, Adonis function) test on the traits x site matrix. Adonis can be used to test for similar means (centroids) of groups. A permutation test is used to determine if the data are consistent with the null hypothesis of no difference of centroids.

Taxonomic richness and FRic were estimated using the accumulation of taxa across sampling events. We combined replicate stream microhabitat invertebrate samples into 1 sample per year

from each hydrologic category for a total of 23 stream samples. We tested the relationship between FRic and taxonomic richness with linear regression. Taxonomic richness was log-transformed to meet the assumption of linearity. Separate linear regression models were run to assess the relationships between responses of FRic and taxonomic richness to hydroperiod within ponds and streams. We tested the effect of ecosystem type on the dependent variables of FRic and taxonomic richness while controlling for the effect of hydroperiod and taxonomic richness by ANCOVA. The slope of the relationship between functional and taxonomic richness determines the degree of functional redundancy in communities, which may differ between habitats. We used the interaction term from ANCOVA to analyze differences in the slopes and intercepts between streams and ponds from regressions of FRic vs. taxonomic richness and FRic and taxonomic richness vs. hydroperiod. If the interaction term was significant, we concluded streams and ponds had different slopes for the relationship tested.

We conducted the following analytical steps on both stream and pond datasets independently and on the combined dataset. First, we calculated trait dissimilarity (quantitative Bray-Curtis) and taxonomic dissimilarity (binary data, Sørensen dissimilarity) between all pairwise combinations of assemblages using R Package software (Vegan, function: vegdist). Second, we calculated distance to centroid ('variation' beta diversity) and tested for homogeneity of multivariate dispersion (betadisper function) between groups (pond vs. stream and intermittent vs. perennial). This method produces an independent dissimilarity value for each sample, distance to group centroid, and has been proposed as an index of beta diversity to express variation in community structure among groups (Anderson 2006, Anderson et al. 2006). Third, we tested for differences in mean trait distances using PERMANOVA (adonis function) on the distance matrices ran with 999 permutations. The adonis function can use both factors (in our case pond vs stream or intermittent vs. perennial) and continuous (hydroperiod) explanatory variables and handles several variables together. Adonis tests for differences in means (centroids) of groups while betadisper tests for differences in dispersion (variation beta diversity). Fourth, we examined turnover beta diversity in both the taxonomic and functional diversity components along a hydroperiod gradient using the distance matrices for invertebrate assemblages and functional traits. We plotted the pairwise dissimilarity distances against the hydroperiod gradient and performed linear regression on the relationship.

8.4 Results

Hydroperiod ranged from 65 to 365 days for ponds and 1 to 365 days for streams. Invertebrate assemblages from streams and ponds shared 14 orders, 34 families, and 6 genera in common (Appendix A). Thus, at the level of genus, ponds and streams in aggregate had only 3.8% of taxa in common.

Trait composition. The two RDA axes significantly explained 54.1% of the total pond and stream invertebrate functional trait structure (permutation test $P = 0.001$). The RDA showed 50.3% of the variance was expressed on axis 1 and identified a gradient that contrasted perennial ponds

and streams occurring in the right side of the ordination from the intermittent ponds and streams that occupied the top left side of ordination (Figure 8.1). Even though the species pools of ponds and streams were notably different, most intermittent sites from both ponds (58%) and streams (82%) converged in the upper left quadrate of the ordination thus, demonstrating trait similarities regardless of ecosystem type. Several traits were tied exclusively to longer hydroperiods, including the use of gills for respiration, lack of diapause ability, and univoltine reproduction. Ponds with longer hydroperiod were more likely to have larger sized taxa (<16 mm) than streams and longer hydroperiod streams were more associated with aerial active dispersal mode. The environmental gradients of hydroperiod and ecosystem showed similar strength of correlation, but in opposite directions (-0.628 and 0.702, respectively) on axis 2. RDA axis 2 (3.8% of variance) further separated ponds and streams and reinforced the pattern of convergence among short hydroperiod sites. The higher trait redundancy in ponds may have contributed to less spread among sites in ordination space. The adonis test confirmed the patterns seen in the RDA in that the trait means (centroids) differed significantly between ponds and streams ($R^2 = 0.14$, $P = 0.01$) and among hydrologic categories ($R^2 = 0.32$, $P = 0.01$). There was also a significant interaction ($R^2 = 0.057$, $P = 0.02$). The centroid locations for intermittent ponds was not significantly different from intermittent streams on axis 1 (Welch Two Sample t-test: t = -1.8199, df = 16.826, $P = 0.087$), but were significantly different on axis 2 (t = -4.2499, df = 14.353, $P = 0.0008$).
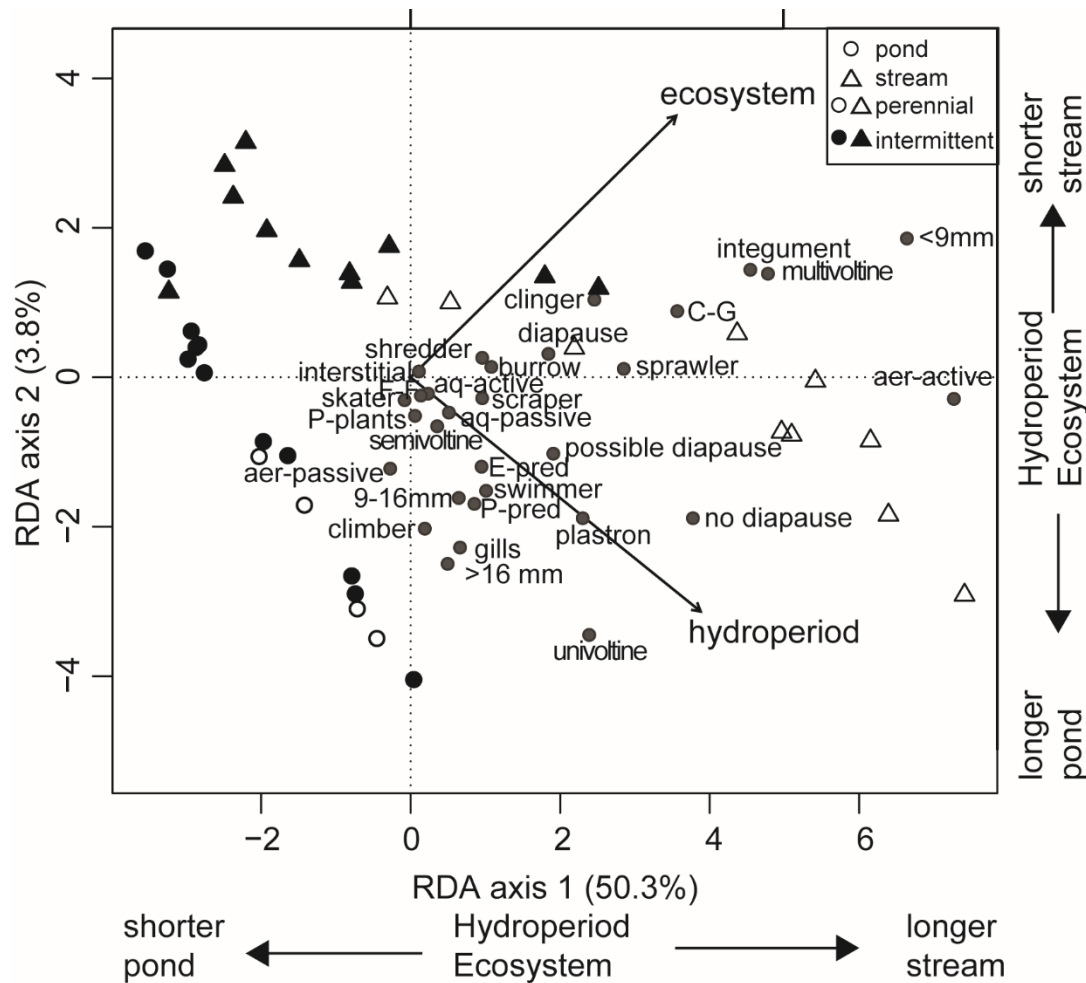
Figure 8.1 Intermittent hydrology produces convergent trait structure in pond (circles) and stream (triangles) invertebrate communities. Bi-plot of the first two axes of the Redundancy Analysis (RDA) illustrating the relationship between predictor variables (n = 2, arrows), sites (n = 37, symbols) and traits (n = 30, grey dots) from invertebrate samples. Sites are coded by hydrologic category based on whether a site experienced a drying period (intermittent, filled triangles and circles) or not (perennial, open triangles and circles).

Functional-taxonomic richness relationship. We found support for the hypothesis that FRic should be positively related to taxonomic richness. Streams and ponds independently showed strong positive relationships between FRic and taxonomic richness (linear regression: ponds: R^2 = 0.825, $F_{1,14}$ = 71.8, P <0.0001; streams: R^2 = 0.927, $F_{1,20}$ = 265.5, P <0.0001). However, there was a significant difference between the slopes of FRic from ponds and streams for any incremental amount of taxonomic richness, in that streams consistently had higher FRic (ANCOVA: P = 0.002; Figure 8.2). Slopes of the relationships indicate higher redundancy in ponds (non-logged slope = 0.093 vs stream = 0.580).

Hydroperiod-richness relationships. We found that invertebrate taxonomic richness was positively related to hydroperiod (lm: R^2 = 0.38, $F_{1,35}$ = 23.15, P <0.0001) and that the slopes of

the regression lines for ponds and streams between hydroperiod and taxonomic richness were not significantly different (ANCOVA: $P = 0.14$; ponds $n = 16$: slope $= 0.06$; streams $n = 21$: slope $= 0.14$), indicating that ponds and streams of the same hydroperiod had similar taxonomic richness and moderate levels of redundancy (Figure 8.3A). By contrast ponds and streams showed different positive relationships between FRic and hydroperiod (ANCOVA: $F_{1,33} = 6.10$, $P = 0.019$; Fig. 3B). In both ponds and streams a lengthening of hydroperiod reflected an increase in occupied niche space (FRic; ponds $R^2 = 0.37$, $F_{1,14} = 9.823$, $P = 0.007$; streams $R^2 = 0.43$, $F_{1,19} = 15.95$, $P = 0.0008$), but ponds had lower FRic than streams at any given hydroperiod (ponds: FRic $= 0.008 \times$ hydroperiod $+ 2.66$; streams: FRic $= 0.08 \times$ hydroperiod $+ 20.72$; Fig. 3B). Therefore, we found support for our hypothesis that ponds and streams would show similar taxonomic richness patterns across a hydroperiod gradient, but we could not accept our hypothesis that ponds and streams would show similar functional richness patterns across a hydroperiod gradient.
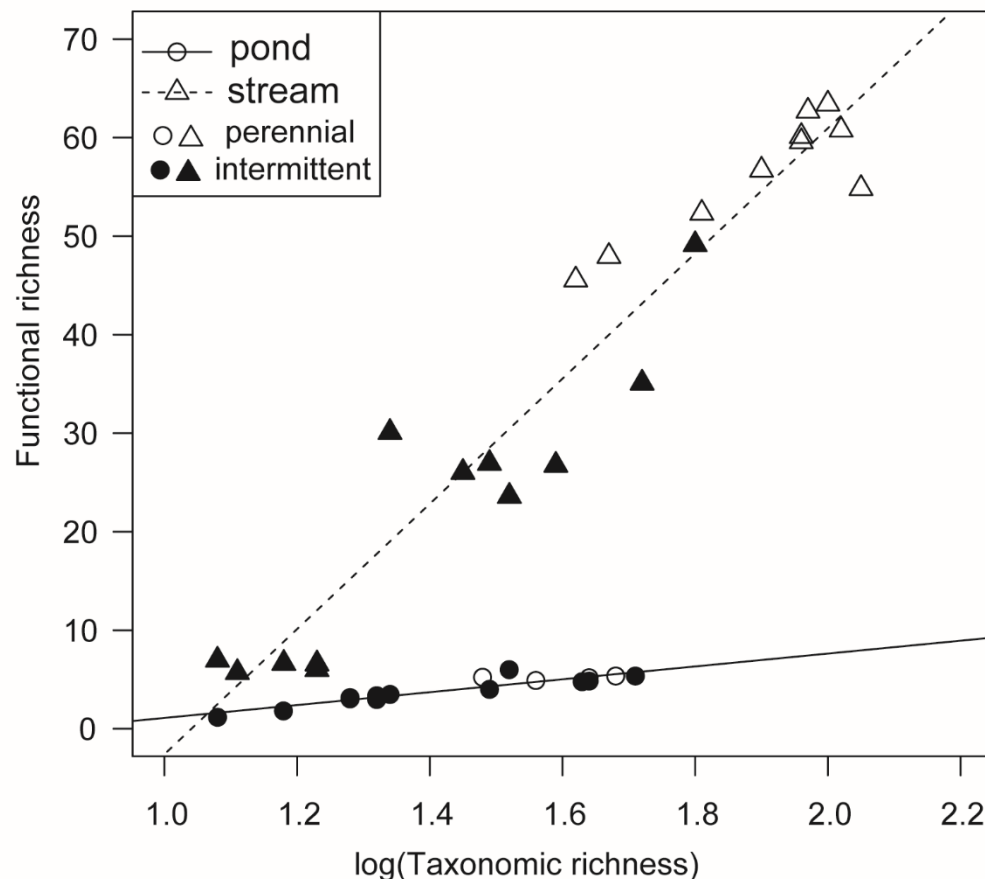

Figure 8.2 The relationships between functional richness and invertebrate taxonomic richness is steeper in streams streams ($n = 23$, FRic $= 63.54$ x $- 66.13$) vs. ponds ($n = 16$, FRic $= 6.53$x $- 5.43$). Pond functional richness values were multiplied by 10 for better graphical presentation.
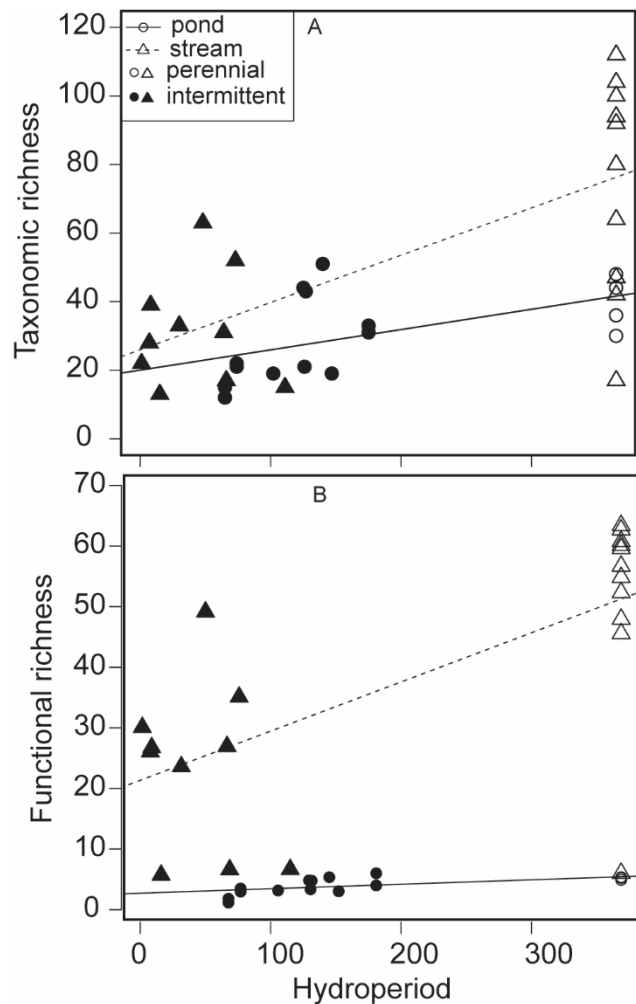
Figure 8.3 Relationship between invertebrate A) taxonomic richness and B) functional richness across hydroperiod gradient. Taxonomic richness slopes do not differ between ponds and streams. FRic is higher in streams and the slope (0.084) differs statistically from slope of the pond FRic-hydroperiod relationship (0.008). Pond FRic values were multiplied by 10 for better graphical presentation.

Beta diversity. Variation beta diversity (distance to centroid) of invertebrate assemblages varied significantly between ponds and streams (homogeneity of multivariate dispersions: $P = 0.004$) and was overall significantly higher in intermittent sites compared to perennial sites (0.56 and 0.44, respectively, F = 6.167, $P = 0.018$; Figure 8.4A). The pairwise comparisons indicated that perennial ponds and streams did not differ in variation beta diversity (permuted $P = 0.34$). However, intermittent sites differed in variation beta diversity from their perennial counterparts (streams: $P = 0.001$; ponds: $P = 0.015$). Mean taxonomic dissimilarities showed significant differences between ponds and streams (PERMANOVA: $R^2 = 0.40$, $P = 0.001$) and between intermittent and perennial habitats ($R^2 = 0.09$, $P = 0.015$).

Trait variation beta diversity was significantly higher in streams compared to ponds (homogeneity of multivariate dispersions: 0.30 vs. 0.20, F = 5.196, $P = 0.015$). However,

intermittent habitats were not significantly different from perennial habitats (0.27 vs. 0.20, F = 3.244, P = 0.07; Figure 8.4B). Intermittent ponds and intermittent streams were similar in terms of high trait variation beta diversity (permuted P = 0.19). Intermittent sites had significantly higher trait variation beta diversity compared to their perennial habitat counterparts (ponds: 0.20 vs 0.09, P = 0.05; streams: 0.27 vs. 0.12, P = 0.03). Mean trait dissimilarities were also significantly different between ponds and streams (PERMANOVA: R^2 = 0.14, P = 0.002) and between hydrologic categories R^2 = 0.29, P = 0.001).

Invertebrate assemblages exhibited relatively little turnover beta diversity (dissimilarity) across the hydroperiod gradient from intermittent to perennial habitats (linear model: $F_{1,28}$ = 0.091, P = 0.06). There was no relationship within streams (R^2 = 0.025, $F_{1,9}$ = 1.267, P = 0.29, CV = 0.15) or ponds (R^2 = -0.14, $F_{1,6}$ = -0.14, P = 0.74, CV = 0.13) across a continuous hydroperiod gradient (Figure 8.5A). Functional trait turnover beta diversity was variable along the hydroperiod gradient and showed a declining pattern compared to invertebrate assemblage turnover (R^2 = 0.11, $F_{1,27}$ = 4.579, P = 0.04; Figure 8.5B). Pond sites showed a decline in beta diversity along the hydroperiod gradient, suggesting perennial ponds were more similar to one another than intermittent ponds were to one another (R^2 = 0.60, $F_{1,8}$ = 14.42, P = 0.005). There was no trend in stream sites (R^2 = -0.027, $F_{1,9}$ = 0.7414, P = 0.411). Overall, ponds had lower trait dissimilarity (mean 0.28) than streams (mean 0.43), indicating pond trait compositions were more similar and had less trait turnover between ponds. Dong et al. (2015) found in a simulation study that turnover beta diversity patterns may be influenced by differences in habitat capacity among sites and suggested using the Chao similarity to make among-site comparisons; however, our results were similar regardless of the similarity index employed.
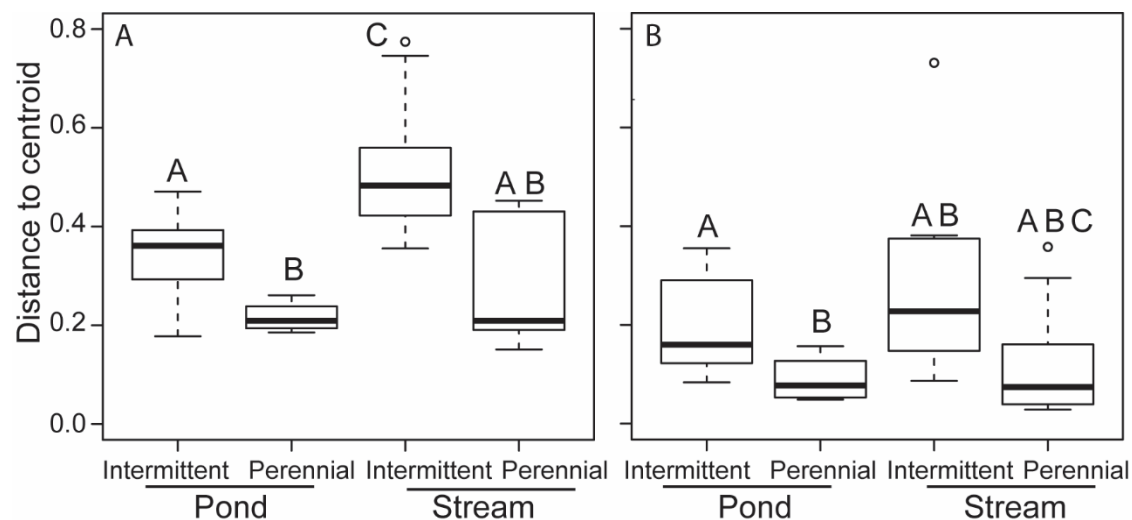

Figure 8.4 Box plot and whiskers plot showing the variation in the distribution of distance to centroid (variation beta diversity) of pairwise comparisons among ponds and streams within each hydrologic category. A) invertebrate assemblages and B) invertebrate functional traits from stream (n = 23) and

pond (n = 16) sites. The letters above the groups indicate pairwise comparisons: groups with the same letter are not significantly different and groups with different letters indicate significant differences in dispersion. Variation beta describes variation in community structure among sample sites from either intermittent or perennial hydrologies. Higher values correspond to greater beta diversity (dispersion).
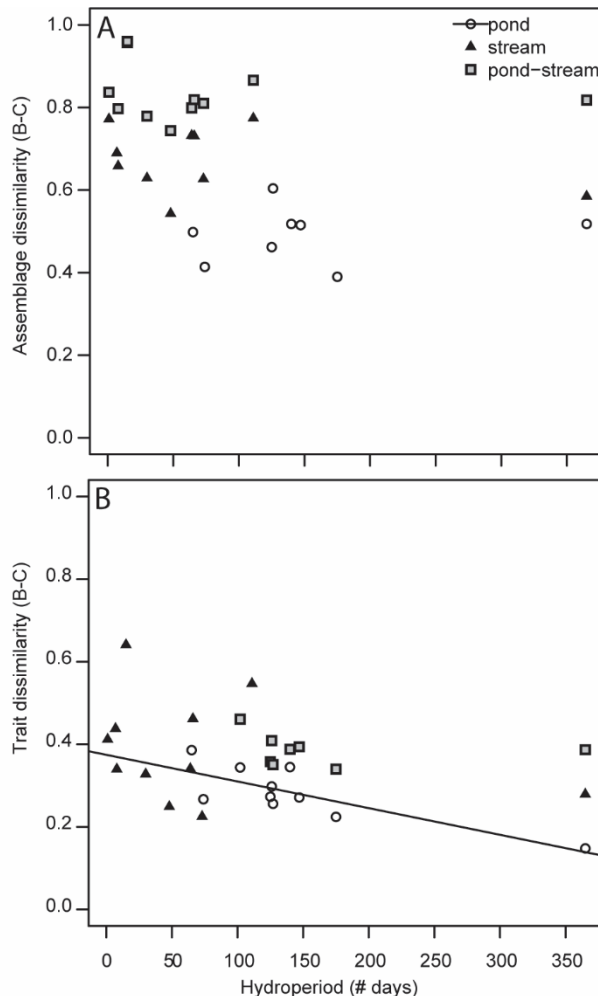

Figure 8.5 The relationship between dissimilarity (turnover beta diversity) of A) invertebrate assemblages and B) functional traits from pond and stream sites along hydroperiod gradient. Each point is the mean pairwise comparison within ponds, within streams, and the between pond-stream comparision. Both y-axes express dissimilarity thus 1 means the two sites do not share any taxa or traits.

8.5   Discussion

Hydrology is one of the primary environmental filters shaping aquatic communities. Fundamental differences in pond versus stream habitats (or a scientists' study preference for one ecosystem over another) have perhaps deterred cross-ecosystem comparisons. However, cross-ecosystem comparisons may indicate ecological patterns and processes in common. We took a

functional trait perspective which allowed the comparison of aquatic invertebrate species compositions from two ecosystems and found that similar hydrologic processes led to similarity in trait composition and beta diversity. Our findings also show that temperate ponds and dryland streams show distinct patterns in their accumulation of functional richness across taxonomic richness and hydroperiod gradients. These results highlight the importance of deterministic processes such as trait filtering, in that short hydroperiods impose similar functional constraints on pond and stream organisms.

We tested whether the relationship between FRic and taxonomic richness was consistent in both ponds and streams. Indeed, each habitat alone showed a positive linear relationship, but differences in their slopes were evident. These differences reveal information about how communities might respond to ecological perturbations. For instance, a positive linear relationship (slope = 1) indicates that species additions to a community result in new ecological functions (low redundancy), as found in rocky reef fish assemblages (Micheli and Halpern 2005). A shallower positive slope (<1) indicates redundancy because some species share functional traits, which has been observed in bird assemblages (Petchey et al. 2007). We found significant positive relationships between FRic and taxonomic richness indicating moderate levels of redundancy (multiple species perform similar functions) in stream and pond invertebrate communities. However, the occupied niche space of ponds was smaller and filled with functionally-redundant species compared to stream sites. Possible reasons for why ponds may have higher redundancy than streams include differences in resource availability, differences the number of functional groups, and the taxonomic resolution of organisms.

Responses of taxonomic richness and FRic to hydroperiod also exhibited positive relationships. Both habitats similarly accumulated taxonomic richness with increasing hydroperiod, but that did not translate the same way in terms of FRic. Ponds accumulated new species more rapidly than accumulating new functions along the hydroperiod gradient from short to long, as shown by minimal change in FRic along gradient, thus exhibiting trait redundancy. Functional redundancy results from strong environmental filtering (Weiher and Keddy 1995) thus limiting trait diversity. More functionally-diverse communities are thought to offer greater resilience and aid in ecosystem recovery in response to environmental change because of greater ecological redundancy (Hooper et al. 2005). From our data, it seems that ponds, especially those with longer hydroperiods may have a better capacity to cope with or resist environmental variation (because higher average FRic) than invertebrate communities in shorter hydroperiod ponds and possibly, as a whole, stream invertebrate communities. Other aspects of the hydrologic regime such as number of drying events, may be important in influencing this pattern.

Biogeographical history can only partly explain differences in species presence across space. There is tremendous variation in size, habitat permanence, environmental conditions, physicochemical properties and climate between the streams and ponds we compared. These extreme environmental conditions are expected to harbor organisms with diverse adaptations to regional and local conditions and contain different species assemblages. Owing to these

environmental differences, species from ponds and streams may respond differently to environmental variation. It is not uncommon to independently study either streams or ponds across different biogeographic scales. For example, studies have found hydrologic parameters to strongly structure fish assemblage traits and life-history patterns in streams from different continents (Lamouroux et al. 2002, Olden and Kennard 2010). However, it is rare to see studies that cross ecosystem types.

A functional trait perspective allowed us to compare communities that differed almost entirely in their regional species pools. We found support for the hypothesis that habitats with similar hydrologic conditions should share species traits. We found that despite differences in ecosystem type (flowing-water vs. still-water) and species pool, invertebrate assemblages from intermittent ponds and streams show similarity in trait structure along the hydroperiod gradient. Therefore, functional traits in intermittent streams and ponds are similarly influenced by hydroperiod. This pattern was likely influenced by the presence of taxa that are resistant to desiccation or resilient to dynamic hydrologic environments. In our analysis we found traits that are known to be associated with resistance to drought, such as small body size, clinger habit (Townsend and Hildrew 1994,Townsend et al. 1997), and diapause capability (Bonada et al. 2007, Mellado Diaz et al. 2008) and traits that confer resilience to hydrologic variation, such as strong dispersal ability (Townsend and Hildrew 1994, Townsend et al. 1997, Vieira et al. 2004, Bogan et al. 2014) and multivoltinism (Townsend and Hildrew 1994) were highly correlated with intermittent stream habitats. Traits more common in longer hydroperiod habitats were aerial passive dispersal, large body size, lack of diapause capability, and univoltine. Our results are generally congruent with those of Cañedo-Argüelles (2015), which found that dispersal ability of organisms strongly influenced community structure of aquatic invertebrates. Logez et al. (2013) similarly found fish assemblage functional structure across Europe to be mostly related to stream physico-chemical factors and less so by geographical location. Our study provides evidence that a traits-based approach combined with other diversity metrics can effectively convey the underlying responses to environmental variation and ecological processes across ecosystems.

The two concepts of beta diversity (i.e., variation among sampling units and turnover in community structure along an environmental gradient) connects biodiversity at the local scale and regional species pool (Whittaker 1972). We saw parallel variation beta diversity patterns in taxonomic assemblages and functional traits indicating higher beta diversity in intermittent ponds and streams. High beta diversity indicates high variation among communities, and we speculate that in our case it stems from high habitat heterogeneity among intermittent sites. Turnover beta diversity is predicted to decline along a gradient of low to high disturbance (i.e., pond permanence, Chase 2003) Here, we predicted turnover to decline along a gradient from long (perennial) to short hydroperiod because habitat permanence acts as a disturbance to those non-resistant taxa. Although dissimilarity was variable, we did not see a decline in turnover beta diversity in invertebrate assemblages across the hydroperiod gradient. It would be interesting to see if the pattern holds after adding sites from the hydroperiod range of 176 to 364. The modest

turnover in functional traits among ponds along the hydroperiod gradient reflects the redundancy described in the richness relationship within ponds. Additionally, FRic was less variable in ponds (33%) and streams (56%) than taxonomic richness (41% vs. 67%, respectively) across the hydroperiod gradient, indicating ecosystem functions are maintained and the relationship is due to turnover of functionally redundant species across the gradient (Villéger et al. 2012, Trigal et al. 2014). Bogan et al. (2013) found that, despite the spatial proximity of headwater perennial stream sites to intermittent stream sites, their invertebrate assemblage composition (turnover beta diversity) was considerably different. We speculate that the hydrologic difference between headwater and nearby intermittent sites was contributing to turnover beta diversity in their study because we also observed similar differences between intermittent (average dissimilarity = 0.72) and perennial streams (0.48). Therefore, even though stream reaches may be connected at certain times of the year, the fact that sections experience drying is a stronger determinant of assemblage and trait structure than spatial proximity.

Congruence of beta diversity and richness hotspots are important for conservation planning (McKnight et al. 2007). We saw higher beta diversity in intermittent habitats, but lower FRic and taxonomic richness in intermittent habitats. This mismatch occurs because traits shift in importance and presence along the hydroperiod gradient. Fewer species may be present in an intermittent habitat, but those species have evolved unique biological traits that enable them to resist dry periods that perennial species do not possess (Lytle and Poff 2004). Additionally, the branching network shape of lotic systems vs. the more isolated nature of ponds may influence dispersal pathways and hence beta diversity.

Understanding how trait composition varies among different geographic areas, organismal groups, and across environmental gradients is of pressing concern in streams (Heino et al. 2013) and may help us identify underlying ecological patterns. Our study addresses this need for research by comparing disparate pond and stream habitats across an environmental gradient, and we have shown that general relationships exist among hydrology, taxonomic diversity, and functional richness regardless of aquatic ecosystem. Aquatic ecosystems may be more susceptible to losses in biodiversity than their terrestrial counterparts (Dudgeon et al. 2006). Therefore, patterns in trait similarity and beta diversity across a hydrologic gradient can be used to inform conservation decisions in a changing climate.

8.6   Acknowledgements

9 Technology transfer

9.1 Summary of data dissemination and technology transfer

We are disseminating the results and findings from our research through a variety of media. Peer-reviewed publications form the intellectual backbone of our endeavor and describe our findings and methods in detail. Presentations at professional meetings provide a further outlet for our research. These presentations reach a broader management-oriented audience at meetings such as the Desert Fishes Council and the Society for Freshwater Science, which are attended by DoD biologists. We are making our data directly available to base managers via our custom-developed graphical user interface, which allows the visualization and inspection of the enormous invertebrate dataset we generated during this project. We will discuss the results of our research alongside a related SERDP-funded project (RC-1724) at a SERDP-sponsored webinar in February of 2017. Finally, we have utilized social media to announce the publication of papers and significant findings, primarily on Twitter (@oldenfish, @mtbogan, @dalytle).

Data dissemination activities

Peer-reviewed publications:	11
Presentations at professional meetings	20
Database	Available to managers as MS Access database
Data visualization tool	GUI for database visualization, now live and online
Webinar for managers	Scheduled for February 2017
Social media	Primarily via Twitter

9.2 Invertebrate database and web-based graphical user interface (GUI)

The full database consists of 339,692 species by site occurrences along with relevant metadata, and is thus a comprehensive and powerful resource for aquatic ecosystem management. A database this large is also difficult to visualize and to use effectively, so we custom-developed a unique platform for database visualization using a web-served GUI. The interactive site is currently housed by the Cosine support team at Oregon State University and is viewable live at:

http://lytle-capstone.science.oregonstate.edu/app/

The GUI interacts with a remote user and the server-housed biodiversity database to produce biodiversity information at any given spatial or taxanomic resolution (Figure 9.1). The interface consists of Map, Filter, and Statistics views with the following attributes:

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Filter View selects information of interest by:

- Date range
- Season
- Biological taxonomy in hierarchy
- Location in hierarchy

Map View displays samples by:

- Region (DoD installation)
- Catchment
- Stream reach
- Individual sample

Graph View displays biodiversity data by:

- Location
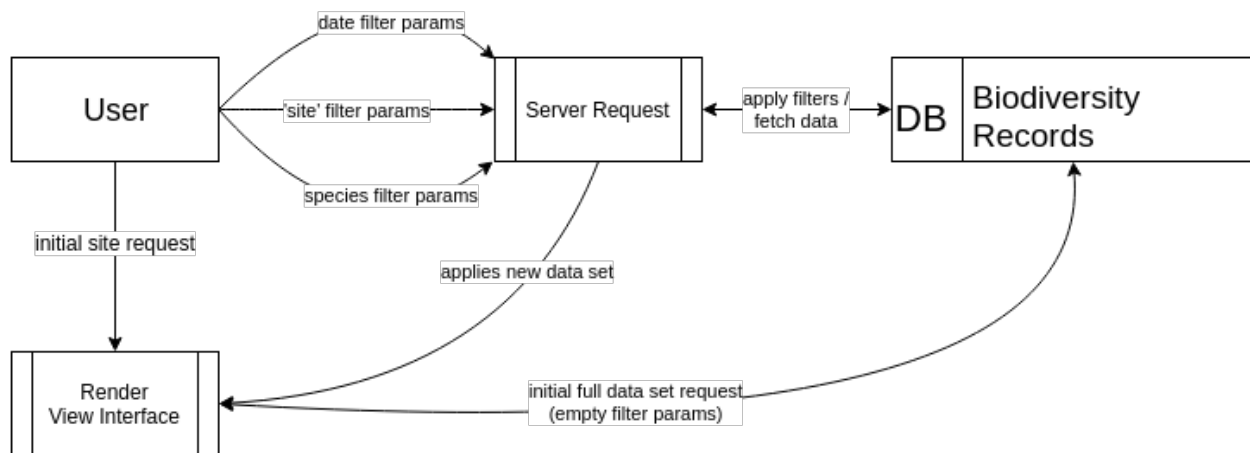- Overall distribution
- Time

Figure 9.1 Data flow schematic for biodiversity data visualization GUI.

Upon page loading, the default view shows all sites, season, and taxa selected, with corresponding statistics (Figure 9.2). Users are then allowed to refine the data search by region or site, with resolution shown as finely as a single sample (Figure 9.3). Users may also select any combination of taxa to be shown, with resolution down to genus or species. If multiple time periods are selected, the GUI will display how biodiversity metrics change through time (Figure 9.4). Depending on the management or research goal, the user may also exclude taxa from view and statistics by checking the appropriate boxes, which results in a censored dataview (Figure

9.5). Names of censored taxa are dimmed in the display, to emphasize the fact that some taxa are being excluded from the analysis.
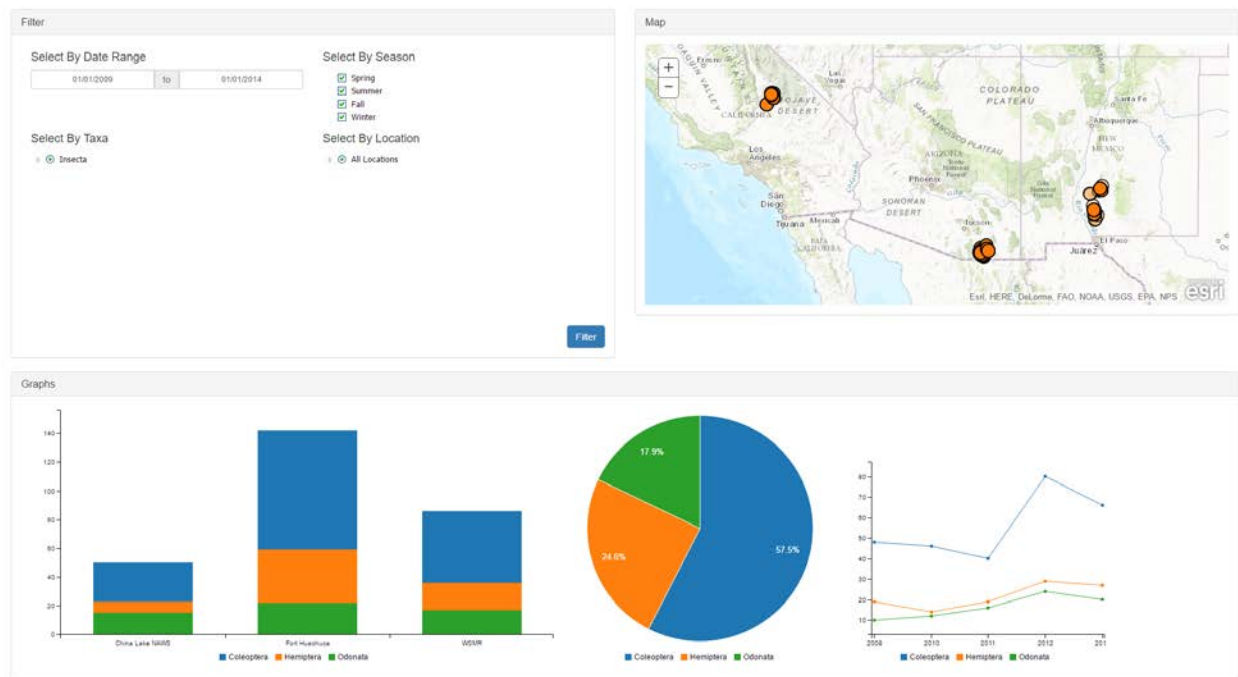

Figure 9.2 An example page load under Filter view, with all data selected.

Figure 9.3 User-changeable filter schematic, showing selection criteria by time, taxa, and location.
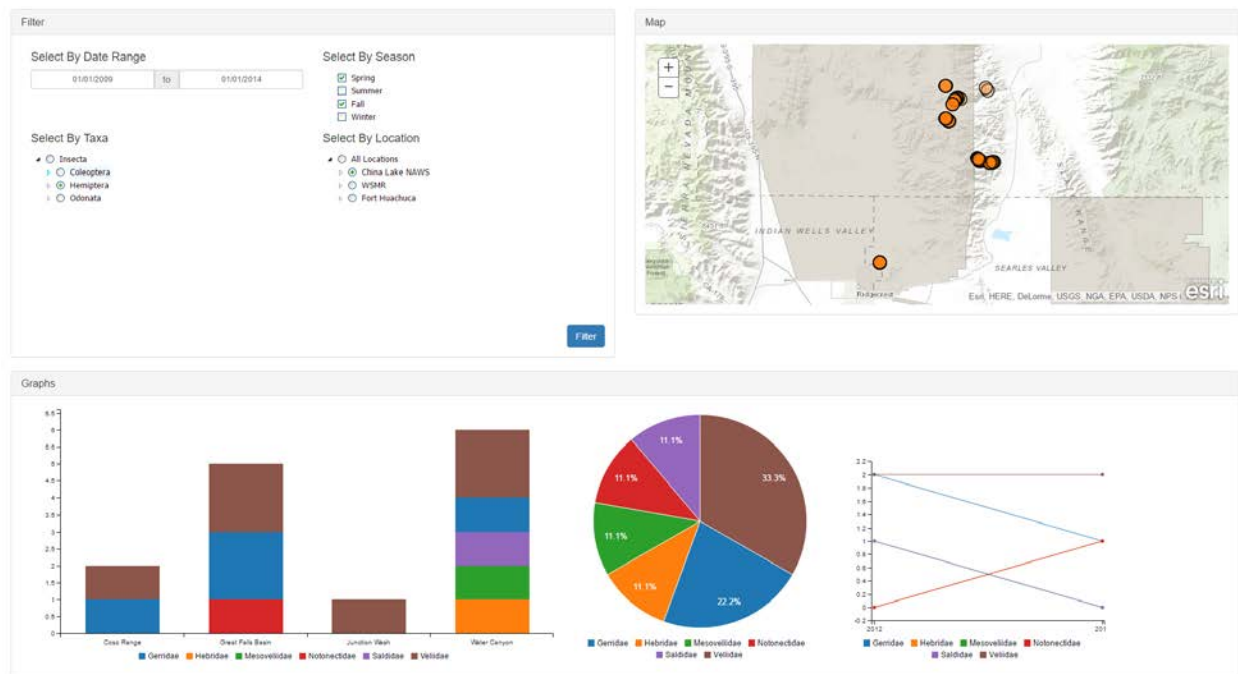
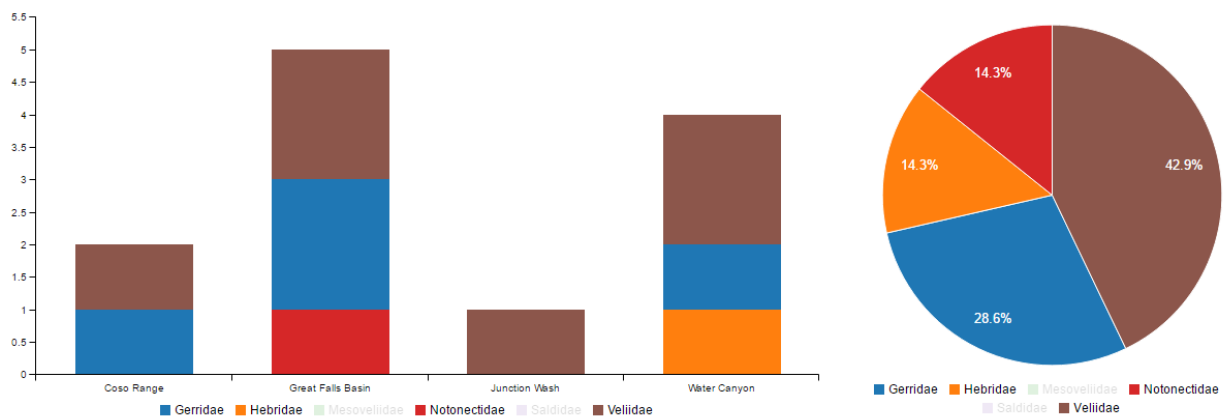Figure 9.4 Filters for refining data in Map and Graph views.

Figure 9.5 Further selection in Graph view allows user to exclude taxa from pie and bar charts.

9.3 Publications

We currently have 11 peer-reviewed publications related to this project. Many of these are in the top-tier ecological journals such as *Ecology* and *Ecosphere.* The extensive invertebrate dataset

generated during this project is being used in a number of collaborative analyses, so we expect the impact of this project to extend beyond the project duration.

2016. Schriever, T.A., and D.A. Lytle. Convergent diversity and trait composition in temporary streams and ponds. **Ecosphere** 7(5). **DOI:** 10.1002/ecs2.1350

2016. Cañedo-Argüelles, M., M.T. Bogan, D.A. Lytle, & N. Prat. Are Chironomidae (Diptera) good indicators of water scarcity? Dryland streams as a case study. **Ecological Indicators** 71: 155-162.

2015. Dong, X., R. Muneepeerakul, J.D. Olden, & D.A. Lytle. The effect of spatial configuration of habitat capacity on beta diversity. **Ecosphere.** DOI: 10.1890/ES14-00497.1

2015. Boersma, K.S., L.E. Dee, S.J. Miller, M.T. Bogan, D.A. Lytle, & A.I. Gitelman. Linking multidimensional functional diversity to quantitative methods: a graphical hypothesis-evaluation framework. **Ecology** 97(3): 583-593. **DOI:** 10.1890/15-0688

2015. Bogan, M.T., K.S. Boersma, & D.A. Lytle. Resistance and resilience of invertebrate communities to seasonal and supraseasonal drought in arid-land headwater streams. **Freshwater Biology** doi:10.1111/fwb.12522.

2015. Schriever, T.A., M.T. Bogan, K.S. Boersma, M. Cañedo-Argüelles, K.L. Jaeger, J.D. Olden, & D.A. Lytle. Hydrology shapes taxonomic and functional structure of desert stream invertebrate communities. **Freshwater Science** doi: 10.1086/680518.

2015. Cañedo-Argüelles, M., K.S. Boersma, M.T. Bogan, J.D. Olden, I.C. Phillipsen, T.A. Schriever, D.A. Lytle. Dispersal strength determines metacommunity structure in a dendritic riverine network. **Journal of Biogeography 42(4): 778-790.** DOI: 10.1111/jbi.12457.

2014. Boersma, K.S., & D.A. Lytle. Overland dispersal and drought escape behavior in a flightless aquatic insect, *Abedus herberti* (Hemiptera: Belostomatidae). **Southwestern Naturalist 59: 301-302.**

2014. Boersma, K.S., M.T. Bogan, B.A. Henrichs, & D.A. Lytle. Top predator removals have consistent effects on large species despite high environmental variability. **Oikos. DOI: 10.1111/oik.00925**

2014. Boersma, K.S., M.T. Bogan, B.A. Henrichs, & D.A. Lytle. Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. **Freshwater Biology** 59: 491-501.

2013. Bogan, M.T., K.S. Boersma & D.A. Lytle. Flow intermittency alters longitudinal patterns of invertebrate diversity and assemblage composition in an arid-land stream network. **Freshwater Biology** 58(5): 1016-1028.

9.4 Presentations to professional societies

Presentation to professional societies is a critical part of the shaping of our ideas, as well as dissemination of findings to the general ecological community and to natural resource managers. Our project findings have been well-represented at basic ecological meetings, such as the Ecological Society of America (ESA) and Society or Freshwater Science (SFS) meetings. We have also presented at management focused meetings such as the Desert Fishes Council (DFC) which are attended by regionally-focused aquatic resource managers, including managers who work on Department of Defense lands.

2016   Lytle, Merritt, Olden, & Tonkin. Society for Freshwater Sciences, Sacramento CA.

Tonkin & 3 others. Society for Freshwater Sciences, Sacramento CA.

2015   Lytle, Merritt & Olden. DoD Climate Change meeting, Boulder CO.

Kennedy & 4 others. International Society for River Science, La Crosse WI.

Lytle & Hartfield Kirk. Desert Fishes Council, Furnace Creek CA.

2014   Lytle & 6 others. Desert Fishes Council, San Jose del Cabo, Mexico.

Lytle & 8 others. Joint Aquatic Sciences Meeting, Portland OR.

Hartfield Kirk and & 4 others. Joint Aquatic Sciences Meeting, Portland OR.

Boersma & 4 others. Joint Aquatic Sciences Meeting, Portland OR.

Schriever & 4 others. Joint Aquatic Sciences Meeting, Portland OR.

Schriever, Williams, & Lytle. ESA, Sacramento CA.

Boersma & 5 others. ESA, Sacramento CA.

Dong, Muneepeerakul, Lytle, & Olden. ESA, Sacramento CA.

Smith, Finch, Lytle, & Merritt. ESA, Sacramento CA.

Lytle. Oregon State University.

2013   Bogan, Boersma, & Lytle. Society for Freshwater Science, Jacksonville FL.

Boersma, Bogan, & Lytle. Society for Freshwater Science, Jacksonville FL.

Schriever, Bogan, Boersma, Munepeerakul, Olden, & Lytle. ESA, Minneapolis MN.

*Boersma, Bogan, & Lytle. ESA, Minneapolis MN (*Buell Award for best student talk)

Bogan, Boersma, & Lytle. ESA, Minneapolis MN.

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